ISSN 0038-3872

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 100 Number 1

BCAS-A100(1) 1–58 (2001) APRIL 2001

SHOUT
SHARE
IT

Southern California Academy of Sciences

Founded 6 November 1891, incorporated 17 May 1907

OFFICERS

Daniel Pondella, *President*
Ralph Appy, *Vice-President*
Susan E. Yoder, *Secretary*
Daniel A. Guthrie, *Treasurer*
Daniel A. Guthrie, *Editor*
David Huckaby, *Past President*
Hans Bozler, *Past President*

BOARD OF DIRECTORS

1998–2001
Kathryn A. Dickson
Donn Gorsline
David G. Huckaby
Robert F. Phalen
Daniel Pondella

1999–2002
Ralph G. Appy
Jonathan N. Baskin
John W. Roberts
Tetsuo Otsuki
Gloria J. Takahashi

2000–2003
James Allen
John Dorsey
Judith Lemus
Martha and Richard Schwartz
Susan E. Yoder

Membership is open to scholars in the fields of natural and social sciences, and to any person interested in the advancement of science. Dues for membership, changes of address, and requests for missing numbers lost in shipment should be addressed to: Southern California Academy of Sciences, the Natural History Museum of Los Angeles County, Exposition Park, Los Angeles, California 90007-4000.

Professional Members	$35.00
Student Members	20.00

Memberships in other categories are available on request.

Fellows: Elected by the Board of Directors for meritorious services.

The Bulletin is published three times each year by the Academy. Manuscripts for publication should be sent to the appropriate editor as explained in "Instructions for Authors" on the inside back cover of each number. All other communications should be addressed to the Southern California Academy of Sciences in care of the Natural History Museum of Los Angeles County, Exposition Park, Los Angeles, California 90007-4000.

Date of this issue 12 April 2001

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

E QH1
.S69
V. 100:1

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

2001 ANNUAL MEETING

May 4–5, 2001

CALIFORNIA STATE UNIVERSITY
AT LOS ANGELES

Symposia:

Nutrient Dynamics in Marine and Estuarine Environments; Dr. Krista Kamer, (SCCWRP), kristak@sccwrp.org—Friday Morning

Dealing with Contaminated Runoff; Dr. John Dorsey, (City of Los Angeles), (213) 847-6347, jdorsey@san.lacity.org—Friday Morning and Afternoon

Spatially Explicit Ecology; Dr. Carlos Robles, CEA-CREST Director (CSULA), (323) 343-2067, crobles@calstatela.edu—Friday Morning and Afternoon

Neuronal Degeneration, Growth and Repair Throughout the Lifespan; Dr. Amelia Russo-Neustadt (CSULA), (323) 343-2074, arusson@calstatela.edu—Friday Afternoon

Virtual Ocean; Dr. Judith Doino Lemus, (University of Southern California), (213) 740-1965; jdlemus@usc.edu—Friday Afternoon

Environmental Chemistry; Dr. Carlos Robles, CEA-CREST Director (CSULA), (323) 343-2067, crobles@calstatela.edu—Saturday Morning and Afternoon

Marine Ecology of Rocky Reefs and Areas of Special Biological Significance; Robert Grove, (Southern California Edison), (626) 302-9735, grovers@sce.com or, Dan Pondella, (Occidental College), (323) 259-2955—Saturday Morning and Afternoon

The Puente-Chino Hills Wildlife Corridor and Wildlife Corridors in the Los Angeles Basin; Dr. Daniel Guthrie, (Claremont Colleges), (909) 607-2836, dguthrie@jsd.claremont.edu—Saturday Morning and Afternoon

CALIFORNIA
ACADEMY OF SCIENCES
MAY 14 2001
LIBRARY

CALL FOR MENTORS

The **Research Training Program** of the Southern California Academy of Sciences is receiving a large number of applications from students for the 2001–2002 academic year. This is in large part due to an excellent article in the **Los Angeles Times** about the program and success of students enrolled in it. The program involves the placement of high school students with excellent scientific backgrounds from throughout southern California in scientific laboratories to conduct research under research mentors. The projects are usually designed by the mentor. Students spend about 8 hours a week on their projects, commencing in September and concluding in May with the presentation of their results at the Annual Meeting of the Academy.

We are seeking scientists who might like to become mentors for these outstanding students in the coming year. If you or your graduate students have room in your lab for a student, please let us know. We need your name, address, contact numbers (include e-mail) and an indication of research area. Forward the above information to:

Dan Guthrie
dguthrie@jsd.claremont.edu
909 607 2836

Bull. Southern California Acad. Sci.
100(1), 2001, pp. 1–11

Pliocene Amphibians and Reptiles from Clark County, Nevada

JIM I. MEAD[1] and CHRISTOPHER J. BELL[2]

[1]*Department of Geology and Quaternary Sciences Program, Northern Arizona University, Flagstaff, Arizona 86011*
[2]*Department of Geological Sciences, University of Texas at Austin, Austin, Texas 78712*

Abstract.—Pliocene herpetofaunas are uncommon in the published literature. Here we report on a small Pliocene (Blancan Land Mammal Age) herpetofauna from the White Narrows local fauna (Clark Co., Nevada) dating approximately 4.9 to 4.3 Ma. At least two species of *Bufo,* a phrynosomatid lizard, *Xantusia,* and a colubrine snake were recovered from sediments deposited in a basin that held a small lake. Climate was probably subhumid, but a cooling and aridification trend was occurring. The vegetation may have been a mosaic of oak-juniper (?) woodland and a riparian community. The White Narrows herpetofauna is depauperate in comparison to the present community which is probably due to sampling bias and not a climatic factor.

In contrast with the mammalian faunas, there are relatively few described amphibian and reptile faunas from the late Tertiary of what is now the Intermountain Region of western North America. This paucity of localities, and the consequent gaps in our understanding of herpetofaunal biogeography and biodiversity in this region renders any new information noteworthy. In this paper we describe the amphibian and reptile components of a small, relatively diverse vertebrate assemblage (White Narrows local fauna) recovered from a locality in Clark County, Nevada, and discuss their biogeographic significance in relation to the changing physiographic setting.

The fossils reported here were recovered from San Bernardino County Museum locality 2.12.16, which was discovered and collected as a result of paleontological mitigation efforts conducted in the late 1980s by the museum along the right-of-way for the Kern River Gas Transmission Line. The locality is situated at 520 m elevation, approximately 2 km south of the Muddy River in Moapa Valley, about 8 km upstream from the confluence with Meadow Valley Wash at Glendale, Clark County, Nevada. The San Bernardino County Museum Regional Paleontologic Locality Inventory places the locality (referred to as Moapa Bluffs) at the SW ¼ of the NE ¼ of the SW ¼ of the SW ¼ of Section 7, T15S, R66E (Mount Diablo Base and Meridian), Moapa West quadrangle, on US Bureau of Land Management holdings. Abbreviations for museums include: MCZ, Museum of Comparative Zoology, Harvard University; SBCM, San Bernardino County Museum; UCMP, University of California Museum of Paleontology.

Overview, Stratigraphic Setting, and Chronology

The establishment of ancient drainage systems in the region of the Muddy River in Moapa Valley in southeastern Nevada were governed by major structural features that developed during the Miocene. These events and their consequences were discussed by Longwell (1936), Lucchitta (1972, 1979, 1990), Dicke (1985), Duebendorfer and Wallin (1991), Schmidt et al. (1996), and Williams (1996). During the Miocene, extensional stress, subsidence, and normal faulting set up the development of the basins and ranges of Nevada and relative uplift of the western margins of the Colorado Plateau. Slow subsidence and basin filling occurred from approximately 24 to 13 Ma. From about 13 to 10 Ma, normal faulting became prevalent, resulting in the rise of mountain ranges and subsidence of basins. In some of these basins, including the one in which the fossils discussed herein were deposited, large lakes and lake systems formed. The ancestral Colorado River began flowing into and through the Muddy Creek basin at approximately 5.5 Ma and ultimately breached the lake basin, establishing external drainage.

Late Tertiary alluvial deposits in the vicinity of Moapa Valley and nearby Meadow Valley received the attention of geologists and paleontologists for many decades. Early studies placed all the sediments into a single unit, the Muddy Creek Formation. Although published reports of fossils from the Muddy Creek Formation exist (Lucchitta 1979; Taylor and Smith 1981; Taylor 1983; Reynolds and Lindsay 1999), remains of fossil vertebrates are relatively uncommon. Vertebrate fossils from the Muddy Creek Formation were first studied by Stock (1921) who assigned the sediments a Mio-Pliocene age based on vertebrate taxa present within the unit.

Recent evaluation of a discrete sedimentary package in the upper portion of the Muddy Creek Formation resulted in a proposal for the recognition of a new formation, tentatively named the White Narrows (Schmidt et al. 1996). This currently informal formation (no description outside of the 1996 Open-File report has yet appeared; see Salvador 1994:23) was described as a white calcic claystone and clayey limestone, with two distinct subfacies: 1) green claystone, and 2) channel fill deposition in degradational channels. A fossiliferous marl bed, 20 cm thick and about 2 m above the base of the formation, produced the mammals described by Reynolds and Lindsay (1999) and the amphibian and reptilian remains presented here (SBCM 2.12.16; see Schmidt et al. 1996). It is this package of vertebrate remains that compose the White Narrows local fauna.

No radiometric dates are available for the White Narrows formation, and age estimates provided by Schmidt et al. (1996) were based on preliminary identifications of the rodents SBCM 2.12.16. Unfortunately, the mammalian biochronology does not provide unambiguous evidence upon which an age can be based. A recent review of the mammalian fauna recovered from the White Narrows local fauna was provided by Reynolds and Lindsay (1999) who suggested that this depositional unit represents a transition from the late Miocene/earliest Pliocene Hemphillian Land Mammal Age to the Pliocene Blancan Land Mammal Age. The small mammals they reported include the murid rodents *Paronychomys* cf. *P. lemredfieldi.*, *Copemys* cf. *C. vasquezi, Peromyscus valensis, Repomys* cf. *R. gustleyi, Calomys* (*Bensonomys*) cf. *C. coffeyi, Calomys* (*Bensonomys*) cf. *C. arizonae, Neotoma* (*Paraneotoma*) cf. *N. vaughani,* and several heteromyid taxa, including *Dipodomys gidleyi, Oregonomys* cf. *O. sargenti,* and undetermined species of *Perognathus* and *Prodipodomys* (Reynolds and Lindsay 1999).

The lack of confident species identifications for most of the rodent taxa in the fauna renders biochronological age estimates difficult. Most of the genera can be found in Hemphillian and Blancan deposits and definitive species identifications are required for refined biochronological age estimates. Of the nine taxa listed by Reynolds and Lindsay (1999) as being "restricted temporally" to either the Hemphillian or Blancan land mammal ages, only two (*Peromyscus valensis* and *Dipodomys gidleyi*) are definitively identified to species. *Peromyscus valensis* is currently known only from the Hemphillian and *D. gidleyi* only from the Blancan. In addition, the shrew genus *Sorex* is represented in the White Narrows local fauna (possibly by two species; see table 3, p. 473, in Reynolds and Lindsay 1999), and is elsewhere known only from Blancan and younger faunas (Repenning 1967; McKenna and Bell 1997). The locality is either of latest Hemphillian age, dating between approximately 6.5 and 4.9 Ma, or is earliest Blancan, dating between approximately 4.9 and 4.3 Ma. The overriding compliment of taxa seems to imply a Blancan age for the fauna, and is therefore the assumed age for this report (this is in agreement with the conclusions of Reynolds and Lindsay 1999).

Systematic Paleontology

All specimens are housed in the Section of Geological Sciences at the San Bernardino County Museum and are catalogued under collection number SBCM L-2515. Each specimen has a separate catalog number. Terminology for anurans follows Tihen (1962) and Sanchiz (1998). Iguanian familial designation follows Frost and Etheridge (1989).

Class AMPHIBIA Linnaeus, 1758
Subclass Lissamphibia Haeckel, 1866
Order Anura Rafinesque, 1815
Family Bufonidae Gray, 1825
Genus *Bufo* Laurenti, 1768
Bufo boreas/canorus/exsul group

Material.—Left ilia 570–571, 2720–2729; right ilia 572, 2730–2734.

Identification.—The dorsal protuberance is relatively high (varies from high to medium-low on the fossils), but the anterior and posterior edges of the protuberance are even with the top of the dorsal prominence (the protuberance does not stand out from the prominence). A distinct, projecting protuberance occurs on the living *B. cognatus, B. microscaphus, B. retiformis,* and *B. woodhousei* and on the extinct *B. hibbardi* and *B. pliocompactilis* (Wilson 1968; Taylor 1941A) implying that our specimens do not belong to any of these species. The extinct *B. suspectus* has a prominence with the posterior slope steeper than the anterior slope; it was assumed by Tihen (1962) to belong to the *B. valliceps* species group and by Estes and Tihen (1964) to belong to the *B. americanus* species group. The specimens listed above have a dorsal prominence similar in size to that described for *B. suspectus,* but do not exhibit the steeper posterior slope. The range of individual variation in this character needs to be thoroughly examined for all North American representatives of *Bufo.*

The ventral acetabulur expansion is not flared out and flattened as on *B. punctatus,* or anteriorly rounded as on *B. debilis* (young and adult specimens). Specimen 571 is not similar in size or in robustness to *B. holmani* (Parmley 1992), nor does it have the medially-directed crest on the dorsal surface near the middle

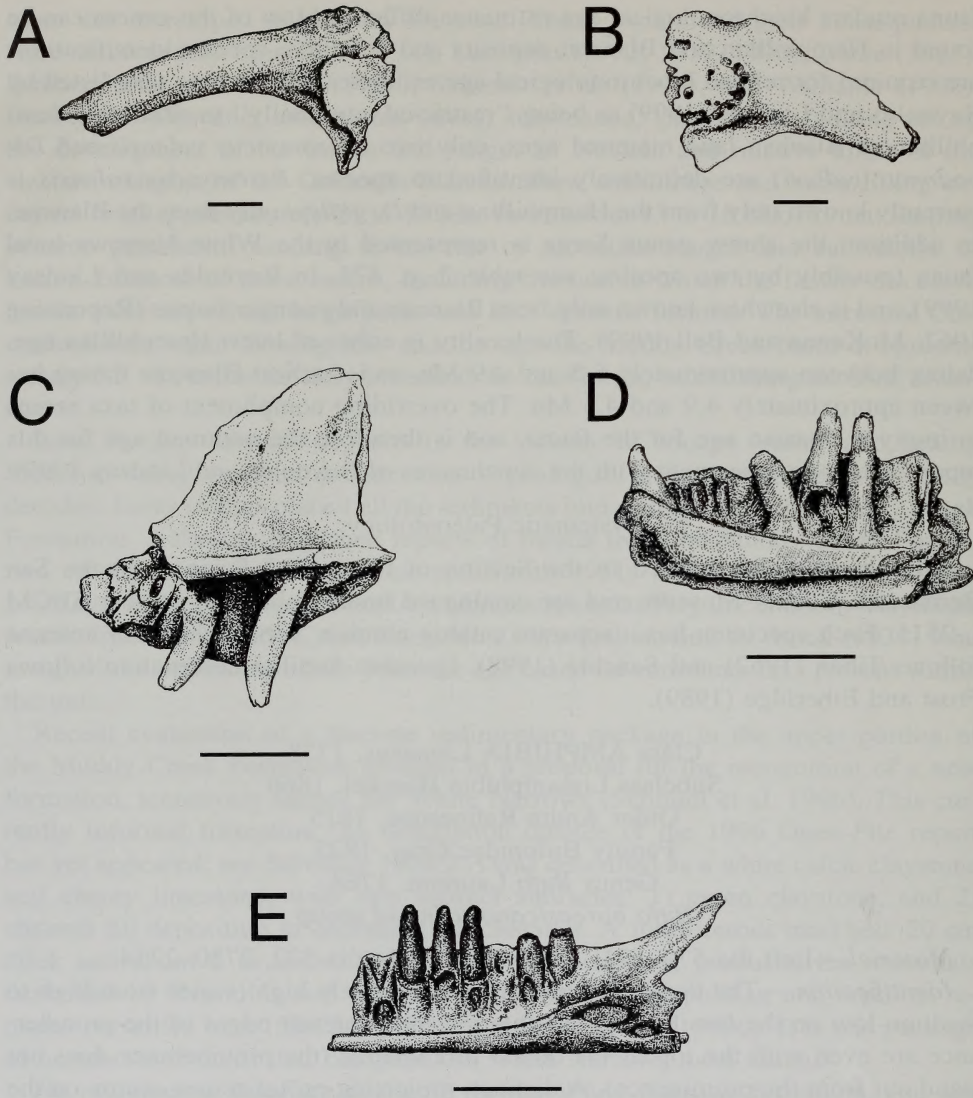


Figure 1. Herpetofaunal specimens from the Blancan White Narrows local fauna, Clark County, Nevada. A, left ilium of *Bufo boreas/canorus/exsul* group, SBCM L2515-571; B, right ilium of *Bufo suspectus,* SBCM L2515-2718; C, right maxilla fragment of Phrynosomatidae indet., SBCM L2515-602; D, right dentary fragment of Phrynosomatidae indet., SBCM L2515-603; and E, right spleniodentary fragment, SBCM L2515-595. Scale bars = 1 mm.

of the shaft as is characteristic of *B. hibbardi* (Taylor 1941A). The prominence and morphology of the protuberance on 571 is identical to living *B. boreas* specimens with an svl of approximately 30 mm. Because the ilia listed above exhibit characters most similar to those found in the *Bufo boreas* species group, we refer our specimens to the *B. boreas/canorus/exsul* group. As indicated above, the White Narrows adult specimens are always small, svl approximately 26 to 40 mm, and in this character resemble more the living toads *B. exsul* and *B. canorus* and not the larger *B. boreas.* Today *Bufo exsul* and *B. canorus* do not live near the Moapa Valley region; *B. boreas* is known from the Muddy River drainage (Stebbins 1985; Hovingh 1997).

Remarks.—Specimen 571 (Figure 1A) is the most complete of the ilia from White Narrows local fauna and is used here as representative of all the specimens referred to this group. The ilium is complete except for the extreme anterior end of the shaft. The overall size of most specimens is that of a toad with a svl (snout-vent length) from 26 to 30 mm (2720 is equal in size to modern toads of svl approximately 40 mm).

Bufo suspectus Tihen, 1962

Material.—Left ilia 2716–2717; right ilia 2718–2719.

Identification.—The low dorsal prominence of the ilium, with the posterior slope steeper than the anterior, and the position of the dorsal protuberance somewhat posterior to the midpoint of the base of the prominence are characteristic for the species. The four ilia listed above all show these features (Figure 1B).

Remarks.—*Bufo suspectus* is a small species of toad originally described from the Blancan Fox Canyon Locality in Kansas (Tihen 1962). Additional material (consisting of a frontoparietal and two ilia) was subsequently recovered from the Miocene Valentine Formation of Nebraska, but was named a distinct species (*B. valentinensis*) on the basis of the supposed geographic and temporal improbability that a species from the Pliocene of Kansas could be the same as a Miocene species of Nebraska (Estes and Tihen 1964). Subsequent reports of "*B. valentinensis*" (e.g., Holman 1970, 1973; Chantell 1971; Parmley 1992) continued this practice, but Sanchiz (1998) recently synonymized the two species under *B. suspectus,* which we endorse.

Bufo sp.

Material.—Angulosplenial 563, 2735–2737; right ilium 573; humerus 564–565, 2738–2743.

Identification.—These specimens were not preserved well enough to permit a more refined identification.

Remarks.—All specimens are from adults of small species of *Bufo* that appear similar in size to living species with svl of approximately 25 to 45 mm.

Class REPTILIA Laurenti, 1768

Order Squamata Oppel, 1811

Family Phrynosomatidae Fitzinger, 1843

Material.—Right maxilla fragment 602; right dentary fragment 603.

Identification.—The fragmentary nature of this material prevents identification beyond the family level. We compared the specimens with modern skeletal material of *Callisaurus, Cophosaurus, Holbrookia, Petrosaurus, Phrynosoma, Sceloporus, Uma, Urosaurus,* and *Uta.* We were unable to detect any derived characters that would permit definitive allocation to any of these taxa, but in their overall size and morphology, the specimens most closely resemble modern specimens of various species in the genus *Sceloporus.*

The difficulties in identifying isolated skeletal elements of *Sceloporus* species were discussed by Etheridge (1964) and Larsen and Tanner (1974). The fossils were compared with modern skeletal material from *S. clarkii, S. graciosus, S.*

jarrovii, S. magister, S. occidentalis, S. olivaceous, S. orcutti, S. poinsettii, S. scalaris, S. undulatus, and *S. virgatus.* Our comparisons failed to reveal any diagnostic features of anterior maxillae or dentaries in extant species, but the fossils are different in some respects from certain species. The teeth are not the relatively heavy, transversely compressed trilobate teeth typical of the extinct *S. robustus* (Twente 1952). The fossils are larger and more robust than modern specimens of *S. graciosus, S. scalaris,* and most *S. virgatus, S. undulatus,* and *S. occidentalis.* The fossil specimens differ from the living *S. clarkii* and *S. orcutti* in that they lack the more pointed, slightly recurved anterior teeth often seen in these two living species. The fossil teeth do not show any trend toward being trilobate and wide, as in modern *S. magister,* however, the robust nature of the anterior portion of the fossil dentary, and the appearance of the dental shelf and meckel's groove are most similar to that species.

Remarks.—The maxilla is a fragmented (3.4 mm long) anterior portion with two blunt conical teeth (Figure 1C). The anterior dentary fragment (3.5 mm long) contains four blunt, conical teeth (Figure 1D).

Family Xantusiidae Baird, 1858

Xantusia Baird, 1858

Material.—L maxilla 591; R spleniodentary 595; R spleniodentary fragment 592, 594, 2744; L spleniodentaries 599-600; L spleniodentary fragments 598, 601.

Identification.—Specimen 595 (Figure 1E) is described here and is representative of the *Xantusia* material from the White Narrows. Specimen 595 is a right spleniodentary with three complete teeth preserved at mid-dentary. The teeth are unicuspate, are of a uniform width at the base and gently taper at the crown. The anterior 10% of the spleniodentary is missing. The dental gutter is well developed.

These fossil specimens are readily identifiable as xantusiids. The White Narrows focal fauna specimens are small, of relatively slight build, and have closely spaced, simple teeth that lack lateral cusps. The splenial appears to be fused with the dentary in all specimens, and does not extend posteriorly beyond the apex of the coronoid in specimens where this character can be evaluated. A pronounced dental gutter is present in all of the spleniodentaries, but there is a varying degree of development in this feature. In all specimens, however, the dental gutter is markedly more developed than in any modern specimens of *Xantusia* examined (Figure 1E).

The small size, slight build, and simple, conical, unstriated teeth of the fossils distinguish them from *Klauberina riversiana* and from the Paleogene genus *Palaeoxantusia.* The dentary teeth of *Lepidophyma* have lingually-directed cusps that superficially resemble, in dorsal view, a mammalian tribosphenic tooth, a feature distinctly lacking in the White Narrows specimens. The limited availability of skeletal material of *Cricosaura typica* makes adequate comparisons impossible at this time, but MCZ 10454 has much more delicately constructed jaw elements than any of the specimens from the White Narrows local fauna. The spleniodentary of *X. henshawi* is longer, more gracile, and has more teeth on average than do the fossil specimens. The fossil specimens are most similar to *Xantusia vigilis,* but are more robust and are slightly longer than the corresponding bones of that species.

A detailed description of an extinct form of *Xantusia* from the Anza-Borrego

Desert in California was provided by Norell (1989). The preserved material shows characteristic plesiomorphic features for the genus, but lacks apomorphies. The plesiomorphic nature of the fossils recovered from Anza-Borrego led Norell to describe *Xantusia downsi** as a new metaspecies (see Gauthier et al. 1988 for explanation of the use of "*" for metaspecies). The White Narrows *Xantusia* specimens are similar to those described by Norell in that they are all characterized by small size, the plesiomorphic presence of a dental gutter, and the synapomorphic reduction of tricuspid teeth. Morphologically, the specimens cannot be distinguished from *X. downsi**, or from numerous other (unpublished) plesiomorphic xantusiids ranging in age from Barstovian (middle Miocene) to early Irvingtonian (early Pleistocene; CJB, pers. obs.). Given the uncertain relationships among plesiomorphic xantusiids, we choose not to identify our material as *X. downsi** and simply refer the specimens to *Xantusia.*

Family Colubridae Oppel 1811
Subfamily Colubrinae Oppel 1811

Material.—Trunk vertebra 618.

Identification.—The specimen conforms to the diagnosis provided by Holman (1979) for colubrine trunk vertebrae. It lacks the hypapophyses characteristic of anterior trunk vertebrae (and those of natricines) and the subcentral paramedian lymphatic fossae characteristic of posterior trunk vertebrae (LaDuke 1991). In overall morphology and proportions, it most closely resembles trunk vertebrae of the 'racers' *Coluber* and *Masticophis.* Auffenberg (1963) provided measurements to distinguish mid-trunk vertebrae of *Coluber* and *Masticophis* in the eastern U.S., but LaDuke (1991) noted geographical variation in Auffenberg's characters. Due to the somewhat poor preservation of this specimen, generic determination is not attempted. Numerous highly fragmented specimens of snake vertebrae were also recovered but are not identifiable.

Discussion and Conclusions

As demonstrated above, the overriding compliment of mammalian taxa seems to imply a Blancan age for the fauna. It appears that the White Narrows local fauna is early Blancan in age (~4.9-4.3 Ma), but probably post-dates the early Blancan Panaca Formation from the nearby Meadow Valley (which dates to about 4.95 Ma; Lindsay et al. 1999; Mou 1999; Reynolds and Lindsay 1999) and predates the well-known Blancan faunas (e.g., Hagerman) of the Glenns Ferry Formation, southern Idaho (see review in Mead et al. 1998).

Vertebrate Faunas

The termination of the Hemphillian Land Mammal Age in the earliest Pliocene is marked by the extinction of most of the typical mammalian species of the late Hemphillian, including taxa with long Miocene histories. The late Hemphillian mammalian faunas suggest that the process of change was taking place at different rates in different geographic regions of North America (Tedford et al. 1987). The accelerating pace of mammalian immigration from Hemphillian into Pleistocene time reflects the availability of dispersal routes into North America and, possibly most importantly, an increase in environmental instability.

The herpetofauna of North America became essentially modern at the familial level during the Miocene (Holman 1995). Many modern families and genera of anurans make their first appearance in North America during the Miocene, including *Bufo, Rana,* Pelobatidae, and Hylidae. Many families of lizards occur, including Iguanidae (sensu lato), Scincidae, Teiidae, Anguidae, Helodermatidae, Xantusiidae, and Rhineuridae. Snakes are represented by five families, including Aniliidae, Boidae, Colubridae, Elapidae, and Viperidae (Holman 1995). These families (except Aniliidae) persist in North America into the Pliocene and through to the Recent. Although Pliocene herpetofaunal records are rare in North America, those available indicate a basically modern fauna (Estes and Baez 1985; Parmley and Holman 1995; Holman 1995).

The majority of the published herpetofaunas of Neogene age from Nevada are late Pleistocene (Rancholabrean) or Holocene in age (Banta 1966; Mead and Bell 1994). At present, our knowledge of late Tertiary herpetofaunas from Nevada is extremely limited. The White Narrows local fauna and deposits located farther north at Panaca, Nevada (Lindsay et al. 1999; Mou 1996, 1997, 1999) appear to be the only sites of this age being studied in the region today. *Scaphiopus alexanderi* was reported from sediments in the Esmeralda Formation of Miocene age (Zweifel 1956) and an undescribed turtle from the same formation was listed by MacDonald and Pelletier (1958). *Miopelodytes gilmorei,* a pelodytid anuran, was described from the middle Miocene of Elko County, Nevada (Taylor 1941B). From localities farther north and west of the White Narrows local fauna, *Rana johnsoni* and *R. plax* were described from sediments that appear to be of Clarendonian to Hemphillian age (upper Miocene; La Rivers 1953, 1966), and an undescribed Clarendonian turtle is included in the Chalk Spring Locality fauna of Elko County (MacDonald and Pelletier 1958). An unidentified snake was recorded from the late Miocene Thousand Creek fauna by MacDonald and Pelletier (1958). A single specimen of snake previously identified as *Coluber/Masticophis* was recovered from Hemphillian sediments in the Truckee Formation of west-central Nevada (Ruben 1971).

The herpetofauna from the White Narrows is not taxonomically diverse. Anurans and a xantusid lizard dominate the fauna. The anurans are expected given the reconstruction of lake, riparian, and oak-juniper (?) open woodland communities nearby (Axelrod 1991; Thompson 1991). The anuran taxa recovered are expected in the region, although species identifications are not precise for most specimens. The recovery of bufonid anurans in the *Bufo boreal canorus/exsul* group might be predicted based on the Recent forms found in the region today (Hovingh 1997), however, this record represents a temporal range extension back to the early Pliocene.

The presence of plesiomorphic *Xantusia* in the White Narrows local fauna is significant for a number of reasons. These specimens represent the northernmost fossil record of the genus reported to date. Norell (1989) reported similar plesiomorphic xantusiids from late Pliocene and early Pleistocene sediments in Anza-Borrego Desert, San Diego County, California. Norell also mentioned that potentially similar forms were present in the Barstow Formation and in Clarendonian age sediments of the Dove Springs Formation of California. Whistler and Burbank (1992) list the Dove Springs Formation material as *Xantusia* sp., and this material resembles (in its plesiomorphy) *X. downsi**. We confirm the presence of plesiomorphic *Xantusia* specimens in at least seven Barstovian deposits in California

(UCMP localities V5501, V6447, V6449, V6463, V65145, V65147, V6604; also SBCM locality 1.130.37, possibly equivalent to UCMP V65147). Fossil material identified as "Iguanidae or Xantusiidae" from the early Miocene Boron Local Fauna in San Bernardino County, California (Whistler 1984) cannot be definitively referred to either taxon at this time; we examined the material and it is too fragmentary to be informative. The geographic and temporal distribution of these fossils raises interesting questions regarding the propriety of allocating geographically and temporally distinct fossils to the same metaspecies. Resolution of this taxonimic problem, and of the systematic position of the fossils in question is beyond the scope of this paper, but will be addressed at a later date.

It would appear from the related data presented above that the basin holding White Narrows sediments contained a lake, with a chemistry permitting the deposition of marl (Schmidt et al. 1996). Climate was probably still subhumid, but a cooling and aridification trend was occurring. Based on assumed reconstructions from the paleobotanical records, this lake might have been surrounded by a mosaic of oak-juniper woodland, possibly other deciduous trees and shrubs, and a riparian community along the lake margins in stream courses. A subhumid climate around a lake with surrounding riparian and open woodland communities would seem ideal for a much more diverse local herpetofauna than was actually recovered. Certainly the lake environment supported a diverse fauna; according to Reynolds and Lindsay (1999) the sediments contained (in addition to the mammals discussed above) remains of perch and sucker fish, gastropods, and ostracods. The low taxonomic diversity is probably due to sampling bias. Additional stratigraphic, paleomagnetic, and paleontologic work is required to better understand the herpetofaunal changes that took place during the Pliocene and immediately prior to the glacial/interglacial phases of the Quaternary.

Acknowledgements

Sue Beard, George Billingsley, Ernie Duebendorfer, Joel Pederson, Dwight Schmidt, and Van S. Williams provided helpful information about the Muddy Creek and White Narrows formations. Eric Scott and Scott Springer helped with locality information for the SBCM material. We thank Jacques Gauthier for insightful discussions about xantusiid lizard evolution. G.E. Swartz provided helpful comments on an earlier version of this report. Figures were prepared by Leigh Anne McConnaughey, for whose patience we are most grateful. We thank Kathy Springer and Betsy Slemmer (SBCM) for assistance with the loan of herpetological remains from the White Narrows local fauna.

Literature Cited

Auffenberg, W. 1963. The fossil snakes of Florida. Tulane Stud. Zool., 10:131–216.

Axelrod, D. I. 1991. The early Miocene Buffalo Canyon flora of western Nevada. Univ. California Publ. Geol. Sci., 135:1–76.

Banta, B. H. 1966. A check list of fossil amphibians and reptiles reported from the State of Nevada. Biol. Soc. Nevada Occas. Pap., 13:1–6.

Chantell, C. J. 1971. Fossil amphibians from the Egelhoff local fauna in north-central Nebraska. Contrib. Mus. Paleontol. Univ. Michigan, 23:239–246.

Dicke, S. M. 1985. Stratigraphy and sedimentology of the Muddy Creek Formation, southeastern Nevada. Unpublished Master of Science thesis, Univ Kansas, 36 pp.

Duebendorfer, E. M., and E. T. Wallin. 1991. Basin development and syntectonic sedimentation associated with kinematically coupled strike-slip and detachment faulting, southern Nevada. Geology, 19:87–90.

Estes, R., and J. A. Tihen. 1964. Lower vertebrates from the Valentine Formation of Nebraska. Am. Midl. Nat., 72:453–472.

Estes, R., and A. Baez. 1985. Herpetofaunas of North and South America during the late Cretaceous and Cenozoic: evidence for interchange? Pp. 139–197 *in* The Great American Biotic Interchange. (F. G. Stehli and S. D. Webb, eds.), Plenum Press, 532 pp.

Etheridge, R. 1964. The skeletal morphology and systematic relationships of sceloporine lizards. Copeia, 1964:610–631.

Frost, D. R., and R. Etheridge. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). Univ. Kansas Mus. Nat. Hist. Misc. Pub., 81:1–65.

Gauthier, J. A., R. Estes, and K. de Queiroz. 1988. A phylogenetic analysis of Lepidosauromorpha. Pp. 15–98 *in* Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp. (R. Estes and G. Pregill, eds.), Stanford Univ. Press, 631 pp.

Holman, J. A. 1970. Herpetofauna of the Wood Mountain Formation (Upper Miocene) of Saskatchewan. Can. J. Earth Sci., 7:1317–1325.

———. 1973. New amphibians and reptiles from the Norden Bridge fauna (Upper Miocene) of Nebraska. Michigan Acad., 6:149–163.

———. 1979. A review of North American Tertiary snakes. Publ. Mus. Michigan State Univ. Paleontol. Ser., 1:200–260.

———. 1995. Pleistocene Amphibians and Reptiles in North America. Oxford Univ. Press, 243 pp.

Hovingh, P. 1997. Amphibians in the eastern Great Basin (Nevada and Utah, USA): a geographical study with paleozoological models and conservation implications. Herpetol. Nat. Hist., 5:97–134.

LaDuke, T. C. 1991. The fossil snakes of Pit 91, Rancho La Brea, California. Los Angeles County Mus. Contrib. Sci., 424:1–28.

La Rivers, I. 1953. A lower Pliocene frog from western Nevada. J. Paleontol., 27:77–81.

———. 1966. A new frog from the Nevada Pliocene. Biol. Soc. Nevada Occas. Pap., 11:6–8.

Larsen, K. R., and W. W. Tanner. 1974. Numeric analysis of the lizard genus *Sceloporus* with special reference to cranial osteology. Gt. Basin Nat., 34:1–41.

Lindsay, E. H., Y. Mou, W. Downs, J. Pederson, T. Kelly, C. Henry, and J. Trexler. 1999. Resolution of the Hemphillian/Blancan boundary in Nevada. J. Vertebr. Paleontol., 19:59A.

Longwell, C. R. 1936. Geology of the Boulder Reservoir, Arizona-Nevada. Geol. Soc. Am. Bull., 47: 1393–1476.

Lucchitta, I. 1972. Early history of the Colorado River in the Basin and Range Province. Geol. Soc. Am. Bull., 83:1933–1947.

———. 1979. Late Cenozoic uplift of the southwestern Colorado Plateau and adjacent lower Colorado River region. Tectonophysics, 61:63–95.

———. 1990. History of the Grand Canyon and of the Colorado River in Arizona. Pp. 311–332 *in* Grand Canyon Geology. (S. S. Beus and M. Morales, eds.), Oxford Univ. Press, 518 pp.

MacDonald, J. R., and W. J. Pelletier. 1958. The Pliocene mammalian faunas of Nevada, U. S. A. Pp. 365–388 *in* Congreso Geologico International, 20th Sesión, Seccion 7 Paleontología, Taxonomía y Evolución.

McKenna, M. C., and S. K. Bell. 1997. Classification of Mammals Above the Species Level. Columbia Univ. Press, 631 pp.

Mead, J. I., and C. J. Bell. 1994. Late Pleistocene and Holocene herpetofaunas of the Great Basin and Colorado Plateau. Pp. 255–275 *in* Natural History of the Colorado Plateau and Great Basin. (K. T. Harper, L. L. St. Clair., K. H. Thorne, and W. M. Hess, eds), Niwot, Univ. Press Colorado, 294 pp.

———, J. T. Sankey, and H. G. McDonald. 1998. Pliocene (Blancan) herpetofaunas form the Glenns Ferry Formation, southern Idaho. Pp. 94–109 *in* And Whereas. . .Papers on the Vertebrate Paleontology of Idaho Honoring John A. White. Volume 1. (W. A. Akersten, H. G. McDonald, D. J. Meldrum, and M. E. T. Flint, eds.), Idaho Mus. Nat. Hist. Occ. Pap., 36, 216 pp.

Mou, Y. 1996. *Mimomys* and *Repomys* (Rodentia: Cricetidae) from the Pliocene Panaca Formation, southeast Nevada. J. Vertebr. Paleontol., 16:55A.

———. 1997. A new arvicoline species (Rodentia: Cricetidae) from the Pliocene Panaca Formation, southeast Nevada. J. Vertebr. Paleontol., 17:376–383.

———. 1999. Biochronology and magnetostratigraphy of the Pliocene Panaca formation, southeast Nevada. J. Vertebr. Paleontol., 19:65A.

Norell, M. A. 1989. Late Cenozoic lizards of the Anza Borrego Desert, California. Los Angeles County Mus. Contr. Sci., 414:1–31.

Parmley, D. 1992. Frogs in Hemphillian deposits of Nebraska, with the description of a new species of *Bufo*. J. Herpetol., 26:274–281.

———, J. A. Holman. 1995. Hemphillian (Late Miocene) snakes from Nebraska, with comments on Arikareean through Blancan snakes of midcontinental North America. J. Vertebr. Paleontol., 15: 79–95.

Repenning, C. A. 1967. Subfamilies and genera of the Soricidae. US Geol. Surv. Prof. Pap., 565:1–74.

Reynolds, R. E., and E. H. Lindsay. 1999. Late Tertiary basins and vertebrate faunas along the Nevada-Utah border. Pp. 469–478 *in* Vertebrate Paleontology in Utah. (D. D. Gillette, ed.), Utah Geol. Surv. Misc. Publ. 99-1, 553 pp.

Ruben, J. 1971. A Pliocene colubrid snake (Reptilia: Colubridae) from west-central Nevada. PaleoBios, 13:1–19.

Ruddiman, W. F., and J. E. Kutzbach. 1989. Forcing of late Cenozoic northern hemispheric climate by plateau uplift in southern Asia and the American west. J Geophys. Res., 94:18409–18427.

Salvador, A. (ed.). 1994. International Stratigraphic Guide: A Guide to Stratigraphic Classification, Terminology, and Procedure, second edition. International Union of Geological Sciences and The Geological Society of America, Inc., 214 pp.

Sanchiz, B. 1998. Encyclopedia of Paleoherpetology, Part 4. Salientia. Verlag Dr. Friedrich Pfeil, 275 pp.

Schmidt, D. L., W. R. Page, and J. B. Workman. 1996. Geologic map of the Moapa West quadrangle, Clark County, Nevada. US Geol. Surv. Open-File Rep. 96-521.

Stebbins, R. C. 1985. Western Reptiles and Amphibians. Houghton Mifflin Company, 336 pp.

Stock, C. 1921. Later Cenozoic mammalian remains from the Meadow Valley region, southeastern Nevada. Am. J. Sci., 202:250–264.

Taylor, D. W. 1983. Late Tertiary mollusks from the Lower Colorado River valley. Contrib. Mus. Paleontol. Univ. Michigan, 26:289–298.

———, and G. R. Smith. 1981. Pliocene molluscs and fishes from northeastern California and norwestern Nevada. Contrib. Mus. Paleontol. Univ. Michigan, 25:339–413.

Taylor, E. H. 1941A. Extinct toads and salamanders from Middle Pliocene beds of Wallace and Sherman Counties, Kansas. State Geol. Surv. Kansas Bull., 38:177–196.

———. 1941B. A new anuran from the middle Miocene of Nevada. Univ. Kansas Sci. Bull., 27:61–69.

Tedford, R. H., M. F. Skinner, R. W. Fields, J. M. Rensberger, D. P. Whistler, T. Galusha, B. E. Taylor, J. R. Macdonald, and S. D. Webb. 1987. Faunal succession and biochronology of the Arikareean through Hemphillian interval (Late Oligocene through earliest Pliocene epochs) in North America. Pp. 153–210 *in* Cenozoic mammals of North America. (M. O. Woodburne, ed.), Univ. California Press, 336 pp.

Thompson, R. S. 1991. Pliocene environments and climates in the western United States. Quat. Sci. Rev., 10:115–132.

Tihen, J. A. 1962. Osteological observations on New World *Bufo*. Am. Midl. Nat., 67:157–183.

Twente, J. W., Jr. 1952. Pliocene lizards from Kansas. Copeia, 1952:70–73.

Whistler, D. P. 1984. An Early Hemingfordian (Early Miocene) fossil vertebrate fauna from Boron, western Mojave Desert, California. Los Angeles County Mus. Contrib. Sci., 355:1–36.

———, and D. W. Burbank. 1992. Miocene biostratigraphy and biochronology of the Dove Spring Formation, Mojave Desert, California, and characterization of the Clarendonian mammal age (late Miocene) in California. Geol. Soc. Am. Bull. 104:644–658.

Williams, V. S. 1996. Preliminary geologic map of the Mesquite quadrangle, Clark and Lincoln counties, Nevada, and Mohave County, Arizona. US Geol. Surv. Open-File Rep. 96-676.

Wilson, R. L. 1968. Systematics and faunal analysis of the lower Pliocene vertebrate assemblage from Trego County, Kansas. Contrib. Mus. Paleontol. Univ. Michigan, 22:75–126.

Zweifel, R. G. 1956. Two pelobatid frogs from the Tertiary of North America and their relationships to fossil and recent forms. Am. Mus. Novitates, 1762:1–45.

Accepted for publication 24 May 2000.

Bull. Southern California Acad. Sci.
100(1), 2001, pp. 12–23

An Evolutionary Classification and Checklist of Amphibians and Reptiles on the Pacific Islands of Baja California, México

L. Lee Grismer

Department of Biology, La Sierra University, Riverside, California 92515-8247

Abstract.—The herpetofauna of the Pacific islands of Baja California is evaluated in light of an evolutionary species concept. Ten subspecies were relegated to synonyms of their peninsular counterparts and three subspecies were elevated to species status.

Resumen.—La herpetofauna de las islas del Pacifico de Baja California está revisada basada en el concepto evolutivo. Éste resultó en la relegación de 10 subespecies al sinónimo a sus contrapartes penínsulares y la elevación de tres subespecies al nivel de especie.

The Pacific coast of Baja California is fringed with a number of islands and small archipelagos. Most are young, relatively small, landbridge islands but others are older and continental or oceanic in origin (Grismer 1993). The herpetofauna of these islands as a whole has received little attention except for the publication of a number of checklists (Bostic 1975; Grismer 1993; Savage 1967; Van Denburgh 1905; Van Denburgh and Slevin 1914; Wilcox 1980; Zweifel 1958) and a biogeographical study of the northern islands (Wilcox 1980). This herpetofauna has never been evaluated taxonomically as a faunal unit.

Subsequent to the latest checklist of this herpetofauna (Grismer 1993), a number of additions (Wong 1997), deletions (Grismer and Hollingsworth 1996; Wong 1997), errors (Aguirre et al. 1999) and/or taxonomic changes (Grismer 1994a, 1999b; Grismer and McGuire 1996; Grismer and Hollingsworth in press; McGuire 1996; Smith et al. 1998; Wong and Grismer in prep.) have been published (Table 1). Additionally, this fauna has never been analyzed in the context of an evolutionary species concept (ESC) as has recently been done for the herpetofauna of the islands in the Gulf of California (Grismer 1999a,b). Grismer (1999b) noted that in the Gulf of California, classifications based on a biological species concept (Mayr 1969) had remained unstable for a number of years. This was because the recognition of insular populations as species or subspecies was largely founded on subjective interpretations of degrees of differentiation even though the data sets being interpreted had remained unchanged. Grismer (1999b) proposed to reduce this subjectivity by employing an ESC (Simpson 1961; Wiley 1978; Frost and Hillis 1990), in which only discretely diagnosable (i.e., no overlap in character state variation) lineages were recognized as species and the subspecies category was abandoned (see Grismer, 1999b for discussion). The subspecies category was not used because its operational duality (i.e., usage for both diagnosable insular populations and portions of continuous continental populations) often misrepresents history. The ESC proved most useful when evaluating insular populations because it divorced decisions of taxonomic rank from subjective interpretations

Table 1. Summary of proposed taxonomic changes used herein. Referenced changes are those that occurred subsequent to Grismer (1993).

Taxonomy of Grismer (1993)	Newly proposed taxonomy
Caudata	
Plethodontidae	
Batrachoseps pacificus major	*B. major* (Wake and Jockusch 2000)
Squamata (Lizards)	
Crotaphytidae	
Gambelia wislizenii copei	*G. copei* (McGuire 1996)
Phrynosomatidae	
Sceloporus magister monserratensis	*S. zosteromus* (Grismer and McGuire 1996)
Uta stellata	*U. stansburiana* (Grismer 1999a; Upton and Murphy 1997)
Gekkonidae	
Phyllodactylus xanti zweifeli	*P. xanti*
Teiidae	
Cnemidophorus tigris multiscutatus	*C. tigris*
Cnemidophorus tigris vividus	*C. tigris*
Anguidae	
Elgaria paucicarinata cedrosensis	*E. cedrosensis* (Grismer and Hollingsworth in prep.)
Elgaria multicarinata ignava	*E. multicarinata*
Elgaria multicarinata nana	*E. nana*
Squamata (Snakes)	
Colubridae	
Chilomeniscus cinctus	*C. stramineus* (Wong and Grismer in prep.)
Diadophis punctatus anthonyi	*D. punctatus*
Hypsiglena torquata baueri	*H. torquata*
Hypsiglena torquata martinensis	*H. torquata*
Lampropeltis zonata herrerae	*L. herrerae*
Masticophis flagellum fuliginosus	*M. fuliginosus* (Grismer 1994a)
Pituophis melanoleucus coronalis	*P. catenifer*
Pituophis melanoleucus fuliginatus	*P. catenifer*
Pituophis vertebralis insulanus	*P. insulanus* (Grismer 1994a)
Crotalus viridis caliginis	*C. caliginis*
Crotalus exsul exsul	*C. ruber* (Smith et al. 1998)

of reproductive compatibility based on degree of differentiation. In instances where subspecies merely delimit the geographic distribution of selected character states within a continuous continental population, there is no evidence that the subspecies represent independent lineages and thus, should not be recognized in a formal taxonomy. This is because the organisms manifesting these character states merely form a co-extensive integrating section of a continuously distributed species. Therefore, it is philosophically illogical and operationally counterproductive to consider arbitrarily defined sections of continuous populations and allopatric diagnosable entities as equivalent phenomenological systems even though both have been traditionally given the rank of subspecies.

It is proposed here that a classification based on the application of the ESC rather than the biological species concept will be more consistent with historical processes because it discourages the recognition of taxa that are not demonstrable evolutionary lineages. Thus, an evolutionary classification is less likely to be misleading to evolutionary biologists working to discover patterns, processes, and/

or adaptations (Brooks and McLennan 1991). Such an interpretation of the Pacific island herpetofauna is warranted.

Species Accounts

The following are discussions of those taxa whose reevaluation under the ESC resulted in changes in their taxonomy. Also treated are published distributional errors not corrected elsewhere in the literature. A summary of the proposed taxonomic changes presented herein and taxonomic changes published subsequent to Grismer (1993) are listed in Table 1. Table 2 lists the species and the islands on which they occur and Appendix I lists the islands and the species that inhabit them. The location of the islands is illustrated in Figure 1.

Caudata

Plethodontidae

Batrachoseps major

Bostic (1975) reported *Batrachoseps major* from Isla San Martín. The specimen was purported to be collected in the late 1970s by Tom Cozens, then a student at San Diego State University (Cozens, pers. comm., 1980). The disposition of the specimen remains unknown.

Anura

Ranidae

Rana pipiens complex

A single specimen of the *Rana pipiens* complex (Los Angeles County Museum [LACM] 91380) was collected from Isla Sur of Islas de Los Coronados on 20 June 1959. No other individuals have been reported. Because there is no permanent water on this island, this specimen is considered a single introduction. Interestingly, three tadpoles (LACM 91381) of the same complex were collected from Punta Banda south of Ensenada opposite Islas Todos Santos on 29 March 1952. No additional specimens from this locality have been reported. Perhaps, during the early fifties, an attempt was made to establish these frogs for commercial purposes.

Squamata (Lizards)

Phrynosomatidae

Urosaurus nigricaudus

In a genetic study of *Urosaurus nigricaudus* from Baja California, Aguirre et al. (1999) included what they believed to be a specimen *U. nigricaudus* from Isla de Cedros (voucher number 1861 of R. W. Murphy). This species, however, has never been reported from Isla de Cedros nor are there any museum records listing its presence despite the numerous collections made from this island in the last 45 years. It is also absent from the adjacent Vizcaíno Peninsula of Baja California (Grismer et al. 1994) to which Isla de Cedros was most recently connected. This record is therefore considered erroneous. The specimen in question, if indeed from Isla de Cedros, is most likely *Uta stansburiana.* This may account for the some of the problems it posed within their data set (Aguirre et al. 1999).

Gekkonidae
Phyllodactylus xanti zweifeli

Dixon (1964) described *Phyllodactylus xanti zweifeli* from islas Magdalena and Santa Margarita on the basis of having a higher number of scales across the snout between the third supralabials (19–22, *n* = 18) as compared to peninsular *P. xanti* (14–21, *n* = 105) as well as having a lower number of scales across the venter (26–33, *n* = 18 vs. 31–41, *n* = 105). However, because the ranges of variation in these counts overlaps with those of peninsular populations, *P. x. zweifeli* is not discretely diagnosable and is recognized here as *P. xanti.*

Teiidae
Cnemidophorus tigris

Cnemidophorus tigris occurs on six islands along the Pacific coast of Baja California (Grismer 1993; Grismer and Hollingsworth 1996). Cope (1892) proposed the name *C. multiscutatus* for the whiptail lizards of Isla de Cedros. Van Denburgh (1894) proposed the name *C. stejnegeri* for populations ranging from Los Angeles, California, southward to near Laguna San Ignacio (see Smith 1946). Subsequent to their descriptions, these two species went through a multitude of taxonomic rearrangements, terminating with Burger (1950) who, without comment, placed both populations under the name *C. t. multiscutatus.* Zweifel (1958) noted that lizards from coastal southern California were very different in striping pattern and coloration from lizards of Isla de Cedros. He stated that it probably was not "proper to refer the two populations to the same subspecies." I have observed living individuals from islas de Cedros and Natividad and found them to be less distinctly striped than lizards from southern California populations but they do form a cline with populations from the adjacent Vizcaíno Peninsula. This is most notable in the dark blotching of the gular and temporal regions where it is prominent in the Vizcaíno Peninsula whiptails, less so in lizards from Isla Natividad, and even less so in lizards from Isla de Cedros. Clinal patterns have been observed in other reptiles through these regions as well (Grismer et al. 1994). Therefore, *C. t. multiscutatus* is not discretely diagnosable and is recognized here as *C. tigris.*

Walker (1981) proposed the name *Cnemidophorus tigris vividus* for the whiptail lizards of islas Norte and Sur of Islas de Los Coronados. He compared a series of lizards from Isla Sur to *C. tigris* of Isla de Cedros, a population from over 500 km to the south, rather than the presumable source population of *C. tigris* from the adjacent peninsula less than 10 km away. Grismer (1994b) noted that the Islas de Los Coronados populations and those from the adjacent mainland overlap in the number of granules around the body (80–100, *n* = 11 vs. 92–116, *n* = 15, respectively), granules between the occiput and rump (167–204, *n* = 11 vs. 192–231, *n* = 15), number of femoral pores (32–40, *n* = 11 vs. 36–43, *n* = 15), and the number of subdigital lamellae on the fourth toe (27–32, *n* = 11 vs. 29–32, *n* = 15). The striping pattern in lizards of the Islas de Los Coronados populations tends to be more vivid but it is not distinct from some individuals of adjacent peninsular populations. Therefore, the Islas de Los Coronados populations are considered here as *C. tigris.*

Table 2. Checklist of the herpetofauna of the Pacific islands of Baja California, México. Asterisks following taxa indicate insular endemics.

Taxon	Insular locale
CAUDATA	
Plethodontidae	
Aneides lugubris	Los Coronados (Isla Norte)
Batrachoseps major	Los Coronados (all islands), Isla San Martín, Todos Santos (Isla Sur)
ANURA	
Bufonidae	
Bufo punctatus	Santa Margarita
Hylidae	
Hyla regilla	Cedros
SQUAMATA (Lizards)	
Crotaphytidae	
Gambelia copeii	Cedros, Magdalena, Santa Margarita
Iguanidae	
Dipsosaurus dorsalis	Magdalena, Santa Margarita
Phrynosomatidae	
Callisaurus draconoides	Santa Margarita
Phrynosoma coronatum	Cedros
Sceloporus occidentalis	Cedros, Todos Santos (Isla Sur)
Sceloporus zosteromus	Cedros, Magdalena, Santa Margarita
Urosaurus nigricaudus	Magdalena, Santa Margarita
Uta stansburiana	Asunción, Cedros, Las Brozas, Las Piedras, Los Coronados (all islands), Magdalena, Natividad, Pata, San Benito, San Gerónimo, San Martín, San Roque, Santa Margarita, Todos Santos (Isla Sur)
Eublepharidae	
Coleonyx variegatus	Cedros, Santa Margarita
Gekkonidae	
Phyllodactylus xanti	Magdalena, Santa Margarita
Teiidae	
Cnemidophorus hyperythrus	Magdalena, Santa Margarita
Cnemidophorus tigris	Cedros, Los Coronados (islas Norte and Sur), Magdalena, Natividad, Santa Margarita
Scincidae	
Eumeces skiltonianus	Los Coronados (islas Norte and Sur), Todos Santos (islas Norte and Sur)
Anguidae	
Anniella geronimensis	San Gerónimo
Anniella pulchra	Los Coronados (islas Norte and Sur), Todos Santos (Isla Sur)
Elgaria cedrosensis	Cedros
Elgaria multicarinata	San Martín
*Elgaria nana**	Los Coronados (islas Norte and Sur)
SQUAMATA (Snakes)	
Leptotyphlopidae	
Leptotyphlops humilis	Cedros
Pythonidae	
Lichanura trivirgata	Cedros, Natividad
Colubridae	
Chilomeniscus stramineus	Cedros, Magdalena
Diadophis punctatus	Todos Santos (Isla Sur), San Martín

Table 2. Continued.

Taxon	Insular locale
Eridiphas slevini	Santa Margarita
Hypsiglena torquata	Cedros, Los Coronados (all islands), San Martín
*Lampropeltis herrerae**	Todos Santos (Isla Sur)
Masticophis fuliginosus	Magdalena, Santa Margarita
Pituophis catenifer	Los Coronados (Isla Sur), San Martín
*Pituophis insulanus**	Cedros
Pituophis vertebralis	Magdalena, Santa Margarita
Salvadora hexalepis	San Gerónimo, Todos Santos (islas Norte and Sur)
Viperidae	
*Crotalus caliginis**	Los Coronados (Isla Sur)
Crotalus enyo	Magdalena, Santa Margarita
Crotalus mitchellii	Santa Margarita
Crotalus ruber	Cedros, Santa Margarita

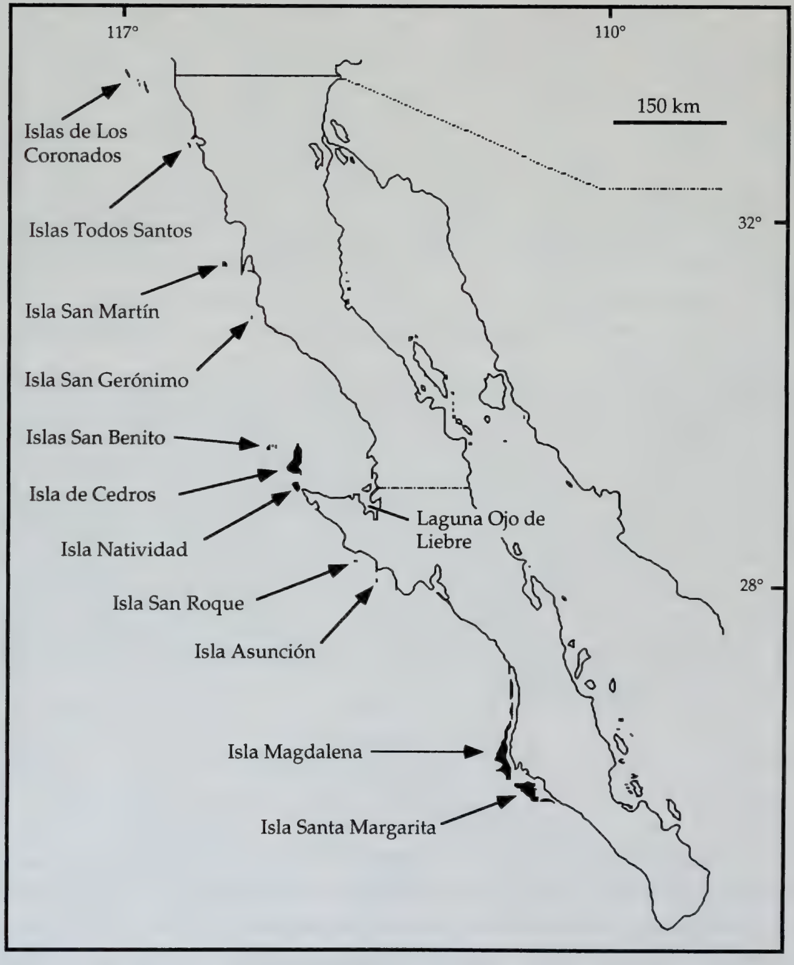

117°
110°
150 km
32°
28°
Islas de Los Coronados
Islas Todos Santos
Isla San Martín
Isla San Gerónimo
Islas San Benito
Isla de Cedros
Isla Natividad
Laguna Ojo de Liebre
Isla San Roque
Isla Asunción
Isla Magdalena
Isla Santa Margarita

Fig. 1. Location of islands along the Pacific coast of Baja California, México.

Anguidae
Elgaria multicarinata

Fitch (1934) separated *Elgaria multicarinata nana* of islas Norte and Sur of Islas de Los Coronados from *E. m. webbi* of San Diego County, California by its smaller size, weak keeling, having fewer transverse ventral scale rows, and subtle differences in the head and body color pattern. However, only adult body size discretely differentiates these two populations, and according to Fitch (1934), "no overlapping size could be shown among the 49 adult specimens from Los Coronados Islands and 35 from San Diego County." Average SVL for *E. m. nana* was 93.3 mm with a maximum SVL of 114 mm and for *E. m. webbi* from San Diego County, average SVL was 135 mm with a maximum of 166 mm (Fitch 1938). Fitch (1938) was aware that body size differences could be the result of an ecological effect imposed by an insular environment rather than a genetically based difference as has been proposed by more recent authors (e.g. Petron and Case 1997 and citations therein). However, Fitch (1938) concluded that the body size differences have a genetic basis, noting ontogenetic changes and sexual dimorphism in *E. m. webbi*-specifically, that the largest individuals have relatively thicker, more heavily keeled scales, and in males, much wider temporal regions. Fitch (1938) pointed out that the largest individuals of *E. m. nana* showed these characters which were indicative of their advanced age even though they were smaller than the small adults of *E. m. webbi.* Additionally, Zweifel (1952) observed a 79 mm SVL female *E. m. nana* copulating, and Burrage (1965) indicated that the hatchling size range of the Islas de Los Coronados population is 32-35 mm SVL, essentially the same as that of hatchling *E. m. webbi* (30-36 mm) from San Diego County, California. This strongly suggests that adulthood, and its accompanied morphological changes, is reached at a much smaller SVL in *E. m. nana* than in *E. m. webbi.* Based on this, *E. m. nana* is recognized here as a distinct species, *E. nana.*

Van Denburgh (1898) described *Elgaria multicarinata ignava* from Isla San Martín as an endemic subspecies characterized by its heavy keeling and darkened dorsal pattern. Fitch (1938), however, noted that an increase in the degree of keeling was a trend that developed in all of the southernmost populations of *E. m. webbi* and did not accord it taxonomic status. Its overall dark color pattern is likely a result of substrate matching, being that it inhabits dark, rocky volcanic habitats. A similar color pattern is found in populations from the volcanic areas of the adjacent peninsular coastline west of San Quintín. Therefore, there are no discretely diagnostic characteristics unique to this population and thus, it is recognized here as *E. multicarinata.*

Squamata (Snakes)
Colubridae
Diadophis punctatus

Van Denburgh and Slevin (1923) proposed the name *Diadophis punctatus anthonyi* for the population on Isla Sur of Islas Todos Santos. This population was diagnosed as having a more robust body (Blanchard 1942) and an obscure neck ring with poorly defined edges (Van Denburgh and Slevin 1923). It is difficult to interpret from Blanchard (1942) how he determined that *D. p. anthonyi* was "larger and stouter-bodied" than adjacent populations of *D. punctatus* because all measurements he gave fall within the range of *D. punctatus* from the adjacent peninsula. Additionally, many specimens from northern Baja California and southern California have a poorly defined neck ring as well. Therefore, this population lacks discretely diagnostic characters and is considered as *D. punctatus.*

Hypsiglena torquata

Zweifel (1958) described *Hypsiglena torquata baueri* from Isla de Cedros on the basis of a number of subtle character state trends of dorsal blotching, nuchal blotching, and the lateral striping on the head. In a review of these snakes, Tanner (1966), noting that these character states overlapped with those occurring in adjacent peninsular populations of *H. torquata,* could not differentiate this subspecies. Based on this, *H. t. baueri* is recognized here as *H. torquata.*

Tanner and Banta (1962) described *Hypsiglena torquata martinensis* on the basis of a single female differentiated from all other Baja California populations in having 54 subcaudals, two loreal scales, and a dorsal scale row formula of 23-21-19-17. Moquard (1899) demonstrated that central peninsular populations of *H. torquata* had 47–58 subcaudal scales and I have observed specimens from the vicinity of Bahía de Los Ángeles with two loreal scales. The diagnostic value of the scale row formula is uninterpretable. Tanner and Banta (1962:24) state that "In *martinensis,* . . .the first fourth of the body has the increase to 23 rows and nearly half have 22 rows. This formula is more nearly the standard pattern for *Hypsiglena,* that is, the greatest number of rows from the nape to near mid-body and then one or more reductions before the vent." Therefore, these characters do not discretely diagnose *H. t. martinensis* and it is considered here a synonym of *H. torquata.*

Lampropeltis zonata

Van Denburgh and Slevin (1923) described *Lampropeltis zonata herrerae* from Isla Sur of Islas Todos Santos. In a revision of *L. zonata,* Zweifel (1952) diagnosed *L. z. herrerae* from all other *L. zonata* by having a combination of no red in the color pattern and the posterior margin of the first white band being anterior to the angle of jaw. This population is often considered as lacking red bands (e.g., Rodríguez-Robles et al. 1999: Fig. 4). However, homologous bands do occur in the anterior portion of the body but are unique in that they have become white or sometimes brownish. Hayes (1975) demonstrated that *L. z. herrerae* had a significantly higher mean number of ventral scales (218.3, 216–220, n = 10) compared to *L. zonata* from the adjacent peninsula (210.4, 207–216, n = 6) and that their ranges only slightly overlapped. Additionally, he showed that the SVL of *L. z. herrerae* averaged over 50 mm larger than the SVLs of southern *L. zonata.* This character state is considered here to be unique because it is the result of an increase in the number and the overall size of the body vertebrae (Hayes 1975). Based on these characteristics, Hayes (1975) recommended that *L. z. herrerae* be elevated to species status. Using mtDNA, Rodríguez-Robles et al. (1999) demonstrated that *L. z. herrerae* is an exclusive population most closely related to individuals of *L. zonata* from the Sierra San Pedro Mártir. Based on the above (excluding ventral scale counts), I elect to follow Hayes (1975) and recognize *L. z. herrerae* as a full species *L. herrerae.*

Pituophis catenifer

Klauber (1946) described *Pituophis catenifer coronalis* from Isla Sur of Isla de Los Coronados on the basis of four specimens. He diagnosed this population as usually having suboculars, frequent abnormalities in the head plates, and fewer number of dorsal blotches. Additionally, he detailed subtle differences from adjacent continental populations of *P. catenifer* in the color pattern of the head. Klauber (1946) also noted, however, that none of these characters discretely separated *P. c. coronalis* from many other subspecies of *P. catenifer* and therefore, this population is recognized here as *P. catenifer.*

Klauber (1946) described and differentiated *Pituophis catenifer fuliginatus* from Isla San Martín from peninsular *P. catenifer* on the basis of having a darker color pattern, large amounts of black spotting on the head, a lower average number of body blotches (62.6, 55–70, n = 15 vs. 75.5, 57–90, n = 52), usually a single instead of two preoculars, a high frequency of aberrant prefrontals, and paired dark subcaudal streaks. Klauber (1946) noted that the overall darkness of the population was probably related to substrate matching and I have observed similarly colored individuals from the volcanic regions west of San Quintín in coastal areas adjacent to Isla San Martín. None of the scale characters discretely separates *P. c. fuliginatus* from adjacent peninsular populations and subcaudal streaking also appears in other *P. catenifer* from Baja California (Klauber 1946). Therefore, this population is recognized here as *P. catenifer.*

Crotalus viridis

Klauber (1949) described *Crotalus viridis caliginis* from Isla Sur of Islas de Los Coronados. Although he could find no differences in color pattern or squamation between it and the adjacent peninsular populations of *C. viridis,* he did note significant differences in body proportions and SVL. Klauber (1949) noted that *C. v. caliginis* would not grow to the size of an average adult *C. v. helleri* of the adjacent peninsula. The largest specimen he measured was 674 mm total length and he notes that *C. v. helleri* regularly reach 1100 mm in length. Also, the rattles of *C. v. caliginis* reach parallelism at a width of 10–11 mm whereas in *C. v. helleri,* parallelism is reached at 15–17 mm (parallelism happens when adulthood is reached). Finally, specimens of *C. v. caliginis* of the same size as *C. v. helleri* have disproportionally smaller heads (Klauber, 1938). Klauber (1949) noted that a 1100 mm *C. v. helleri* "would have 5 times the bulk" of a 650 mm *C. v. caliginis.* Based on these data, *C. v. caliginis* is considered here to be a distinct species, *C. caliginis.*

Acknowledgments

For comments on the manuscript and/or discussions of species concepts I thank B. Hollingsworth, H. Wong, and E. Mellink. I wish to thank K. Beaman for assistance with *Rana* records of the Los Angeles County Museum.

Literature Cited

Aguirre L., G. D. J. Morafka, and R. W. Murphy. 1999. The peninsular archipelago of Baja California: a thousand kilometers of tree lizard genetics. Herpetologica 55:369–381.

Blanchard, F. N. 1942. The ring-neck snakes, genus *Diadophis.* Bull. Chicago Acad. Sci. 7:1–144.

Bostic, D. L. 1975. A Natural History guide to the Pacific Coast and North Central Baja California and Adjacent Islands. Biological Educational Expeditions, San Diego, California.

Brooks, D. R., and D. A. McLennan. 1991. Phylogeny, Ecology, and Behavior. A Research Program in Comparative Biology. University of Chicago Press, Chicago, Illinois, U.S.A.

Burger, W. L. 1950. New, revived, and reallocated names for North American whiptailed lizards, genus *Cnemidophorus.* Natur. Hist. Misc. 65:1–9.

Burrage, B. R. 1965. Notes on the eggs and young of the lizards *Gerrhonotus multicarinatus webbi* and *G. m. nanus.* Copeia 1965:512.

Cope, E. D. 1892. A synposis of the species of the teiid genus *Cnemidophorus.* Trans. Amer. Phil. Soc. 17:27–52.

Dixon, J. R. 1964. The systematics and distributions of the lizards of the genus *Phyllodactylus* in North and Central America. New Mexico State University Res. Center Sci. Bull. 64–1:1–139.

Fitch, H. S. 1934. New alligator lizards from the Pacific coast. Copeia 1934:6–7.

———. 1938. Systematic account of the alligator lizards (*Gerrhonotus*) in the western United States and Lower California. Amer. Midl. Natur. 20:381–424.

Frost, D. R., and D. M. Hillis. 1990. Species in concept and practice: herpetological applications. Herpetologica 46:87–104.

Grismer, L. L. 1993. The insular herpetofauna of the Pacific Coast of Baja California, México. Herpetol. Natur. Hist. 1:1–10.

———. 1994a. The origin and evolution of the peninsular herpetofauna of Baja California, México. Herpetol Natur. Hist. 2:51–106.

———. 1994b. The evolutionary and ecological biogeography of the herpetofauna of Baja California and the Sea of Cortés, México. Ph.D. Diss., Loma Linda University, Loma Linda, California.

———. 1999a. Checklist of amphibians and reptiles on islands in the Gulf of California, México. Bull. Southern California Acad. Sci. 98:45–56.

———. 1999b. An evolutionary classification of reptiles on islands in the Gulf of California, México. Herpetologica 55:446–469.

——— and B. D. Hollingsworth. 1996. *Cnemidophorus tigris* does not occur on Islas San Benito, Baja California, México. Herpetol. Rev. 27:69–70.

——— and B. D. Hollingsworth. In press. A taxonomic review of the endemic alligator lizard *Elgaria paucicarinata* (Squamata: Anguidae) of Baja California, México with a description of a new species. Herpetologica.

——— and J. A. McGuire. 1996. Taxonomy and biogeography of the *Sceloporus magister* complex (Squamata: Phrynosomatidae) in Baja California, México. Herpetologica 52:416–427.

———, J. A. McGuire, and B. D. Hollingsworth. 1994. A report on the herpetofauna of the Vizcaíno Peninsula, Baja California, México with a discussion of its biogeographic and taxonomic implications. Bull. So. California Acad. Sci. 93:45–80.

Hayes, M. P. 1975. The taxonomy and evolution of *Lampropeltis zonata.* Master's Thesis. California State University, Chico.

Klauber, L. M. 1938. A statistical study of the rattlesnakes. Occ. Pap. San Diego Soc. Natur. Hist. 4: 1–53.

———. 1946. The gopher snakes of Baja California, with descriptions of new subspecies of *Pituophis catenifer.* Trans. San Diego Soc. Natur. Hist. 11:1–40.

———. 1949. Some new and revived subspecies of rattlesnakes. Trans. San Diego Soc. Nat. Hist. 11:61–116.

Mayr, E. 1969. Principles of Systematic Zoology. McGraw Hill, New York, New York.

McGuire, J. A. 1996. Phylogenetic systematics of crotaphytid lizards (Reptilia: Iguania: Crotaphytidae). Bull. Carnegie Mus. Nat. Hist. 32:1–143.

Mocquard, F. 1899. Contribution à la faune herpètologique de la Basse Californie. Nouv. Arch. Mus. Nat. Hist. 4:297–344.

Petron, K., and T. J. Case. 1997. A phylogenetic analysis of body size evolution and biogeography in chuckwallas (*Sauromalus*) and other iguanines. Evolution 51:206–219.

Rodríguez-Robles, J. A., D. F. DeNardo, and R. E. Staub. 1999. Phylogeography of the California mountain kingsnake, *Lampropeltis zonata* (Colubridae). Mol. Ecol. 8:1923–1934.

Savage, J. M. 1967. Evolution of the insular herpetofauna. In: Proceedings of the Symposium on the Bology of the California Islands, pp. 219–227. Santa Barbara Botanic Garden, Inc.

Simpson, G. G. 1961. Principles of Animal Taxonomy. Columbia University Press, New York, New York.

Smith, H. M. 1946. Handbook of Lizards of the United States and Canada. Comstock Publishing Associates, Ithaca, New York.

———., L. E. Brown, D. Chizar, L. L. Grismer, G. S. Allen, A. Fishbein, B. D. Hollingsworth, J. A. McGuire, V. Wallach, P. Strimple and E. A. Liner. 1998. *Crotalus ruber* Cope, 1892 (Reptilia, Serpentes): Proposed precedence of the specific name over that of *Crotalus exsul* Garmen, 1884. Bull. Zool. Nomen. 55:1–4.

Tanner, W. W. 1966. The night snakes of Baja California. Trans. San Diego Soc. Nat. Hist. 14:189–196.

———. and B. H. Banta. 1962. Description of a new *Hypsiglena* from San Martín Island, México, with a resumé of the reptile fauna of the island. Herpetologica 18:21–25.

Upton, D. E., and R. W. Murphy. 1997. Phylogeny of the side-blotched lizards (Phrynosomatidae: *Uta*) based on mtDNA sequences: support for a midpeninsular seaway in Baja California. Molecular Phyllogenetics and Evolution 8:104–113.

Van Denburgh, J. 1894. Description of three new lizards from California and Lower California with a note on *Phrynosoma blainvillii.* Proc. Calif. Acad. Sci. 2:296–301.

———. 1898. The *Gerrhonotus* of the San Lucan Fauna, Lower California, with diagnosis of other west American species. Proc. Acad. Nat. Sci. Philadelphia 1898:63–66.

———. 1905. The reptiles and amphibians of the islands of the Pacific coast of North America from the Farallons to Cape San Lucas and the Revilla Gigedos. Proc. Calif. Acad. Sci. 4:1–41.

——— and J. R. Slevin. 1914. Reptiles and amphibians of islands of the west coast of North America. Proc. Calif. Acad. Sci. 4:129–152.

——— and J. R. Slevin. 1923. Preliminary diagnoses of four new snakes from Lower California, Mexico. Proc. Calif. Acad. Sci. 13:1–2.

Wake, D. B. and E. L. Jockusch. 2000. Detecting species borders using diverse data sets: examples from plethodontid salamanders in California. In: The Biology of Plethodontid Salamanders (Eds. R. C. Bruce, R. G. Jaeger, and L. D. Houck), pp. 95–119. Kluwer Academic/Plenum Publishers, New York.

Walker, J. M. 1981. A new subspecies of *Cnemidophorus tigris* from south Coronado Island, Mexico. J. Herpetol. 15:193–197.

Wilcox, B. A. 1980. Species number, stability, and equilibrium status of reptile faunas on the California islands. In: The California Islands: Proceedings of a Multidisciplinary Symposium (Ed. by D. M. Power), pp. 551–564. Santa Barbara Museum of Natural History, Santa Barbara.

Wiley, E. O. 1978. The evolutionary species concept reconsidered. Syst. Zool. 29:76–80.

Wong, H. 1997. Comments on snake records of *Chilomeniscus cinctus, Crotalus exsul* and *C. mitchellii* from Islas Magdalena and Santa Margarita, Baja California Sur, México. Herpetol. Rev. 28: 188.

Wong, H and L. L. Grismer in prep. . . Geographic variation and taxonomy in the sand snakes, *Chilomeniscus* (Squamata: Colobridae)

Zweifel, R. G. 1952. Notes on the lizards of the Coronados Islands, Baja California, Mexico. Herpetologica 8:9–11.

———. 1958. Results of the Puritan-American Museum of Natural History expedition to western Mexico. 2. Notes on the reptiles and amphibians from the Pacific coastal islands of Baja California. Amer. Mus. Nat. Hist. 1895:1–17.

Accepted for publication 1 March 2000

Appendix I

Checklists of the herpetofauna of the islands along the Pacific coast of Baja California, México. Asterisked taxa are insular endemics.

Isla Asunción. *Uta stansburiana.*

Isla de Cedros. *Hyla regilla, Gambelia copei, Phrynosoma coronatum, Sceloporus zosteromus, Sceloporus occidentalis, Uta stansburiana, Coleonyx variegatus, Cnemidophorus tigris, Elgaria cedrosensis*, Leptotyphlops humilis, Lichanura trivirgata, Chilomeniscus stramenius, Hypsiglena torquata, Pituophis insulanus*, Crotalus ruber.*

Isla Las Brozas. (Within Laguna Ojo de Liebre). *Uta stansburiana.*

Isla Las Piedras. (Within Laguna Ojo de Liebre). *Uta stansburiana.*

Isla Magdalena. *Dipsosaurus dorsalis, Gambelia copei, Sceloporus zosteromus, Urosaurus nigricaudus, Uta stansburiana, Phyllodactylus xanti, Cnemidophorus hyperythrus, Cnemidophorus tigris, Chilominescus stramenius, Masticophis fuliginosus, Pituophis vertebralis, Crotalus enyo.*

Isla Natividad. *Uta stansburiana, Cnemidophorus tigris, Lichanura trivirgata.*

Isla Pata. (Within Laguna Ojo de Liebre). *Uta stansburiana.*

Isla San Gerónimo. *Uta stansburiana, Anniella geronimensis, Salvadora hexalepis.*

Isla San Martín. *Batrachoseps major, Uta stansburiana, Elgaria multicarinata, Diadophis punctatus, Hypsiglena torquata, Pituophis catenifer.*

Isla San Roque. *Uta stansburiana.*

Isla Santa Margarita. *Bufo punctatus, Callisaurus draconoides, Dipsosaurus dorsalis, Gambelia copei, Sceloporus zosteromus, Urosaurus nigricaudus, Uta stansburiana, Coleonyx variegatus, Phyllodactylus xanti, Cnemidophorus hyperythrus, Cnemidophorus tigris, Eridiphas slevini, Masticophis fuliginosus, Pituophis vertebralis. Crotalus enyo, Crotalus mitchellii, Crotalus ruber.*

[1]**Islas de Los Coronados.** (Three major islands). *Aneides lugubris* (Isla Norte), *Batrachoseps major, Uta stansburiana, Eumeces skiltonianus* (islas Norte and Sur), *Cnemidophorus tigris* (islas Norte and Sur), *Elgaria nana** (islas Norte and Sur), *Anniella pulchra* (islas Norte and Sur), *Hypsiglena torquata, Pituophis catenifer* (Isla Sur), *Crotalus caliginis** (Isla Sur).

[2]**Islas San Benito.** (Three islands). *Uta stansburiana.*

[3]**Islas Todos Santos.** (Two islands). *Batrachoseps major, Sceloporus occidentalis, Uta stansburiana* (islas Norte and Sur), *Eumeces skiltonianus* (islas Norte and Sur), *Anniella pulchra, Diadophis punctatus, Lampropeltis herrerae**, *Salvadora hexalepis.*

---

[1] Includes all three major islands (islas Sur, Norte, Medio) unless noted otherwise. Isla Medio consists of two small islets: a larger southern islet and a smaller northern islet. No records are known from the latter.

[2] Includes all three islands.

[3] Presence on Isla Sur only unless indicated

Bull. Southern California Acad. Sci.
100(1), 2001, pp. 24–35

Spot Pattern of *Girella nigricans,* the California Opaleye: Variation among Cohorts and Climate Periods

Jana L. D. Davis

Scripps Institution of Oceanography, University of California at San Diego,
9500 Gilman Drive 0208, San Diego, California, 92093-0208

Abstract.—*Girella nigricans* (California opaleye) exhibits variability in dorsolateral spot pattern. Southern California opaleye usually have one pair of white spots; however, fish with additional spots are frequently observed. Additional spots are thought to result from gene flow with the six-spotted Gulf of California *Girella simplicidens.* In the present study, the proportion of fish with extra spots was compared among and within nine *G. nigricans* cohorts settling from 1997 to 1999. This proportion was variable among the nine cohorts. When analyzed by climate regime, cohorts settling during the 1997–98 El Niño event had significantly higher proportions of multi-spotted fish than "normal" and La Niña cohorts. Within five of nine cohorts, the proportion of fish with additional spots significantly increased through time during the study, suggesting that survivorship of multi-spotted fish was greater than that of two-spotted fish during the juvenile stage. The easily identifiable spot polymorphism of *Girella nigricans* provides a useful tool by which to study hybridization between two marine fishes and track changes in gene flow and gene expression over time.

The distribution of nearshore marine populations is often partly determined by abiotic factors. Gradients in temperature, for example, are important on several spatial scales, from meter-scale intertidal zonation (Nakamura 1976) to latitudinal distribution on the kilometer-scale (Morris 1960). Changes in temperature on different temporal scales can affect species' distributions as well. The daily temperature cycle plays a role in meter-scale cross-shore movements of fish (Gibson et al. 1998), seasonal temperature changes force vertical habitat shifts in motile intertidal species (Zander et al. 1999), and temperature variation on scales longer than a year shapes alongshore distribution of nearshore populations (Barry et al. 1995). Over a 60-year period during which water temperature increased by 0.75°C, Barry et al. (1995) found increases in abundance of southern species and decreases in northern species at a California rocky intertidal site, suggestive of range shifts to the north.

Interannual temperature cycles on scales shorter than 60 years, such as that driven by the El Niño Southern Oscillation (ENSO), may also influence species ranges. During warm El Niño events, a rise in water temperature results in shifts of many species to higher latitudes (Arntz and Tarazona 1990). A similar range shift might be expected for hybrid zones where reproductive isolation of species is incomplete. One such zone occurs in Baja California in the region of overlap between *Girella nigricans* (California opaleye) and *Girella simplicidens* (Gulf opaleye). *Girella nigricans* occurs mainly from Cabo San Lucas, Baja California to San Francisco and has one pair of lateral white spots flanking its dorsal fin

(Thomson et al. 1979). *Girella simplicidens* occurs in the Gulf of California to Cabo San Lucas and has three or four pairs of white spots (Thomson et al. 1979; Robins et al. 1991). Although listed as separate species based on dentition, body shape, and spot number, this status may not be warranted morphologically or genetically (Orton and Buth 1984), and genetic exchange between the two groups produces individuals with three, four, and five spots in various lateral arrangements (see Orton et al. 1987).

The forces driving hybridization between marine fish species are poorly understood (Rao and Lakshmi 1999). Reports of marine fish hybrids are much rarer than those of freshwater fish hybrids, due to both a lower tendency of marine fish to hybridize as well as mistaken classification of hybrids as distinct species (Hubbs 1955; Rao and Lakshmi 1999). Possible conditions favorable to marine hybridization include outnumbering of one closely related species by another, intergradation in the parental species' habitats, and environmental disturbances (Rao and Lakshmi 1999). The relative contribution of these conditions to specific hybridization cases, like that of *G. nigricans* and *G. simplicidens,* have not been adequately addressed (Rao and Lakshmi 1999). Questions pertaining to the location of the *G. nigricans-G. simplicidens* hybrid zone, the validity of species-level distinction, the frequency of interbreeding, the fertility of the hybrid offspring, and hybrid variability among others, remain and warrant further study.

One *Girella* hybrid study has addressed the relationship between latitude and the number of three-, four-, five-, and six-spotted fish (referred to hereafter as "multi-spotted") within the *G. nigricans* range (Orton et al. 1987). Lower proportions of multi-spotted fish were found at three southern California sites than at Miller's Landing, Baja California. The presence of such a gradient was attributed to a higher level of genetic exchange between *G. nigricans* and *G. simplicidens* at southern latitudes closer to *G. simplicidens'* range (Orton et al. 1987). If El Niño and other warm water events cause species' ranges to shift to higher latitudes, this gradient of multi-spotted opaleye abundance might also be expected to shift to higher latitudes. At fixed points in California, which are north of the peak region of genetic exchange between the two *Girella* groups, such a range shift might be observed as local increases in the proportion of multi-spotted individuals.

The purpose of the present study was to address the temporal variability in opaleye spot pattern in San Diego, California. Specific goals were to (1) test whether the frequency of spot patterns varied among cohorts recruiting at different times, (2) determine whether spot pattern differed among climate regimes in which the cohorts settled (El Niño, "normal," or La Niña), and (3) determine whether the proportion of multi-spotted individuals within a cohort changed over time, indicating differential survivorship.

Methods

Opaleye and their spot patterns were sampled at two sites in San Diego, California, USA: False Point, in La Jolla (117.3°W, 32.8°N), and Dike Rock, 500 m north of the SIO Pier in the Scripps Coastal Reserve (117.3°W, 32.9°N). After a two- to three-month planktonic larval stage, opaleye generally occupy tidepools for one or two years or until they reach 75 mm total length (Norris 1963; Stevens et al. 1989). Juvenile opaleye are most frequently found in middle to high intertidal pools from 30–90 cm above mean lower low water (MLLW) in San Diego (Davis 2000b). After their intertidal stage, they abandon the intertidal zone in favor of subtidal areas.

Opaleye at False Point were collected from a set of 55 tidepools ranging from 6 cm below MLLW to 107 cm above MLLW. Each tidepool was bailed or siphoned to permit collection of all fish present. Rocks were removed, and each pool was thoroughly searched. Opaleye were collected, their total lengths (TL) and standard lengths (SL) were measured in mm, and the number of spots on each side was recorded. The pool was then refilled, and the fishes were returned. About 4 to 8 days were needed to sample all 55 tidepools. Data were collected during 12 sampling periods: May 1997, August 1997, November 1997, February 1998, May 1998, June 1998, August 1998, October 1998, November 1998, February 1999, March 1999, and August 1999. In August 1999, spot patterns were measured only for opaleye collected from the largest False Point tidepool.

At Dike Rock, opaleye spot pattern was scored in one large tidepool (52 cm above MLLW) from May through October of three years: 1997, 1998, and 1999. This study pool, used by Norris (1963) for behavioral observations of opaleye, is the largest permanent tidepool in the reserve, measuring 4.5 m long, 1.5 m wide, and about 40 cm maximum depth. Opaleye in the pool were collected with minnow traps one to three times per week on average during each May-to-October period, a period that included most opaleye recruitment and therefore highest abundances. From May 25–August 4, 1997, one 40 cm minnow trap with 2 mm mesh and openings of 2.8 cm was deployed for 60 min on each sampling day. On all dates after August 4, 1997, a second trap, with 6 mm mesh and 4 cm openings, was added. The traps were baited with canned cat food and placed in fixed locations in the tidepool. All opaleye collected were measured (TL and SL), their spot pattern was identified, and they were released back into the pool.

Minnow traps were used only at Dike Rock because its pool, much larger than the False Point pools, harbored more opaleye than the False Point pools. At False Point, traps did not capture enough individuals for analysis. In addition, traps were easier to use than the method of draining pools, permitting more frequent sampling at Dike Rock.

Opaleye cohorts were identified from size-frequency histograms and from the arrival of prejuveniles to the study areas. Prejuveniles, characterized by silvery sides, green dorsal surfaces, and the absence of spots, transform into juveniles within a few days of settlement (Stevens et al. 1989). During this transformation period, they turn an olive color and attain their characteristic spots, which are fixed in number during an individual's lifetime (Orton et al. 1987). In general, prejuveniles supplying each cohort identified in the study arrived over an approximately two-week period, followed by a period of absence of prejuveniles. Each cohort was identified at or within a month of settlement, with the exception of one cohort that settled during winter 1998 at Dike Rock, a period when fish were not sampled at this site. Settlement period for this winter cohort was estimated based on the mean size of its fish (64 mm TL) when sampling began in May 1998. For all summer cohorts at Dike Rock, settlement period was determined by the arrival of prejuveniles. Settlement period for each False Point cohort was estimated from periodic (approximately every 2–3 months) size-frequency histograms and when possible, the presence of prejuveniles. Cohorts were followed through time at False Point until they left the intertidal zone and followed at Dike Rock either until they left the intertidal zone or until the end of October of their settlement year.

The proportion of multi-spotted opaleye (P_M) per weekly period was calculated as:

$$P_M = N_M/(N_T - N_{PJ})$$

where N_M is the number of fish with more than two spots collected during a 7-day period, N_T is the number of total fish collected, and N_{PJ} is the number of prejuveniles (fish with undeveloped spots). P_M was calculated over a weekly period instead of daily because the percentage of multi-spotted fish was generally on the order of 5–10%, and on some occasions fewer than 10 fish were caught per day. Therefore, daily data were combined on weekly intervals to avoid zero values and artificially high values driven by low sample size. At False Point, spot proportions were calculated for each cohort using N_M, N_T, and N_{PJ} summed across all 55 study pools. No pool was sampled more than once, but because from three to six days were needed to sample all 55 pools, it is possible that fish moved between pools from day to day resulting in some fish being resampled. At Dike Rock, P_M was calculated for all fish within a cohort caught within a 7-day period. Because data were always collected from the same pool, it is likely that many of the same fish were caught day after day. However, the frequency of recaptures was not expected to be different for two-spotted and multi-spotted fish at either site. Therefore, although the data are not independent, they are not expected to be biased with regard to the hypotheses. For statistical analyses, these values were subjected to arcsin square root transformation.

To determine whether cohorts settling during different climate periods ("normal," El Niño, or La Niña) had different P_M values, each cohort was assigned to a climate period based on temperature and sea level data measured at Scripps Pier. According to temperature and sea level anomalies, the El Niño period began in late summer 1997 and continued through about May of 1998. The La Niña period was in its early stages in August 1998 and continued through the end of the study (Lynn et al. 1998).

To address the question of whether the cohorts had significantly different values of P_M, a one-way analysis of variance (ANOVA) was used to test the difference in average weekly spot proportions among all nine cohorts. Normality of the data was examined using Lilliefors test of residuals ($p > 0.05$). ANOVAs were also used to test whether P_M was different among cohorts within each of the three climate periods. To determine whether spot proportion was different among climate periods, an ANOVA was used with average weekly spot proportion for each cohort within a climate period as replicates. A nested ANOVA with cohort nested within climate period would have provided the most appropriate test to address these questions. However, because different numbers of cohorts were measured during the three climate periods, a nested design was not possible.

To address the question of whether spot proportion changed within cohorts over time, regression analysis was used. In these models, weekly P_M was the dependent variable and time served as the independent variable. To determine whether the proportion of three-spotted fish (P_3) was greater than the proportion of four-spotted fish (P_4) within cohorts, a paired t-test was used.

Table 1. Settlement and size of the nine study cohorts: Cohorts are identified by site (DR = Dike Rock and FP = False Point) and are named by season of settlement (sum = summer, win = winter), the last two digits of the year in which they settled, and their order if more than one cohort settled during a season (1 = first to settle, 2 = second to settle). Dates of settlement and climate type at time of settlement (NORM = normal, EN = El Niño, and LN = La Niña) are listed. The time period over which each cohort was followed and average total length (mm) of fishes at the start and end of that time period are presented.

			Climate	Sampling dates		Avg. fish size	
Site	Cohort	Settlement	type	Start	End	Start	End
DR	sum 97 1	mid-Jun—end-Jun 1997	NORM	Jun 8 97	Oct 14 97	28.0	81.1
DR	sum 97 2	mid-Jul—end-Jul 1997	NORM	Jul 9 97	Oct 18 97	30.0	48.4
FP	sum 97	Jun—Jul 1997	NORM	Jun 20 97	May 15 98	28.8	78.0
DR	win 98	Jan or Feb 1998	EN	May 25 98	Nov 6 98	64.4	94.0
FP	win 98	Feb 1998	EN	Feb 15 98	May 2 99	33.7	88.0
DR	sum 98 1	mid-Jun—end-Jun 1998	NORM	Jun 8 98	Nov 6 98	29.8	60.3
DR	sum 98 2	mid-Aug—end-Aug 1998	LN	Aug 19 98	Nov 6 98	24.8	46.2
FP	sum 98	Aug 1998	LN	Aug 1 98	Aug 20 99	32.0	74.6
DR	sum 99	mid-Jul—end-Aug 1999	LN	Jul 11 99	Oct 26 99	30.6	49.8

Results

During the study, 4012 spot number and configuration scores were taken on post-prejuvenile *Girella*: 1569 at Dike Rock in 1997, 1335 at Dike Rock in 1998, 493 at Dike Rock in 1999, and 615 at False Point from May 1997 to August 1999. As in Orton et al. (1987), most individuals were two-spotted. Of the multi-spotted fish captures, there were 203 scores of three-spotted fish, 118 scores of four-spotted fish, 7 scores of five-spotted fish, and 2 scores of six-spotted fish

From opaleye size frequencies at the two sites, nine cohorts were identified throughout the study period: three at False Point and six at Dike Rock (Table 1). At False Point, cohorts settled in summer 1997, winter 1998, and summer 1998. The summer 1997 cohort was actually produced by two recruitment events, one occurring in late June 1997 and one in late July. However, although they were distinct during August 1997, they were not identifiable in subsequent sampling months and therefore were combined into one cohort for analysis.

At Dike Rock, two cohorts settled in summer 1997 (Figure 1), three were identified from summer 1998, and one cohort settled in summer 1999. One 1998 cohort was greater than 60 mm TL in May of that year, and therefore it likely settled at about the same time as the winter 1998 False Point cohort. The other two 1998 cohorts settled during the summer. Although cohorts that appeared at the same time at the two sites were possibly part of a large scale "meta-cohort," they were considered separate cohorts in the present study. Because some cohorts settled at different times than others, and because cohorts probably abandon their tidepool nursery areas at different times, not all cohorts were followed over the same size ranges (Table 1).

The proportion of multi-spotted fish (P_M) varied among the nine cohorts (ANOVA: $F_{8,72} = 5.12$, $p \ll 0.001$) (Figure 2). However, within the El Niño and La Niña climate periods, P_M was not significantly variable among cohorts (ANOVA: El Niño, $F_{1,11} = 2.18$, $p = 0.168$; La Niña, $F_{2,23} = 0.50$, $p = 0.612$). P_M of the four normal cohorts was variable ($F_{3,38} = 6.42$, $p = 0.001$); however, for the

Table 2. Regression analyses of the number of multi-spotted fish within a cohort versus time. Cohorts are identified and named as in Table 1. The number of total spot measurements of fish within each cohort, as well as the number of weeks for which spot data were taken, are listed.

Site	Cohort	No. measurements	No. weeks	Slope	r^2	p-value
DR	sum 97 1	841	11	$+8.0 \times 10^{-3}$	0.43	0.028
DR	sum 97 2	728	12	$+4.1 \times 10^{-3}$	0.32	0.055
FP	sum 97	196	5	-0.3×10^{-3}	0.04	0.749
DR	win 98	176	8	$+27.4 \times 10^{-3}$	0.70	0.010
FP	win 98	179	5	$+4.4 \times 10^{-3}$	0.26	0.380
DR	sum 98 1	938	14	$+11.0 \times 10^{-3}$	0.64	<0.001
DR	sum 98 2	221	9	$+8.8 \times 10^{-3}$	0.27	0.156
FP	sum 98	240	6	$+1.7 \times 10^{-3}$	0.80	0.016
DR	sum 99	493	11	$+5.9 \times 10^{-3}$	0.26	0.111

"normal" cohort that settled during the period between El Niño and La Niña (June 1998), El Niño conditions prevailed during most of its larval stage. Without this cohort, which had a relatively high average weekly P_M (11.8%), the pre-El Niño cohorts did not exhibit variation in weekly P_M ($F_{2,25} = 1.34$, $p = 0.281$).

Mean weekly proportion of multi-spotted fish in a cohort was significantly different among climate periods (normal, El Niño, and La Niña) (ANOVA: $F_{2,6} = 6.47$, $p = 0.032$; Figure 2). Cohorts recruiting during the El Niño period had higher mean values of P_M (mean of mean P_M = 20.4%) than those recruiting during the normal periods (6.7%) (a posteriori Fisher's LSD; $p = 0.009$) and the La Niña period (7.8%) (a posteriori Fisher's LSD; $p = 0.013$). Spot proportions of the normal and La Niña cohorts were not significantly different from each other ($p = 0.886$).

P_M tended to increase over time within cohorts (Figure 3). This increase was significant in 5 cohorts: 1997 summer 1, 1997 summer 2, 1998 winter, and 1998 summer 1 cohorts at Dike Rock, and the summer 1998 cohort at False Point (Table 2). Within cohorts, the proportion of three-spotted fish was greater than the proportion of four-spotted fish (Table 3). Two-spotted fish were most abundant, followed by three-spotted fish, then by four-spotted fish.

Discussion

Hundreds of three- and four-spotted and several five-spotted *Girella* individuals were observed in San Diego from 1997 to 1999. However, only two *Girella* individuals with six spots, individuals that may have been genetically "pure" *G. simplicidens,* were observed. The rarity of juvenile *G. simplicidens* suggests that adult *G. simplicidens* were not common in the San Diego area. Therefore, multi-spotted fish in the present study were probably not the result of *G. nigricans-G. simplicidens* hybridization occurring within the San Diego region. Instead, high numbers of fish with three and four spots suggests either that 1) hybrid larvae were transported north, or 2) alleles or series of alleles coding for extra spots were present in San Diego populations. The present study does not permit rejection of either hypothesis; however, results of the present study do indicate that processes controlling presence of multiple-spotted fish are variable over time. The frequency of multi-spotted fish varied temporally, both among cohorts and within

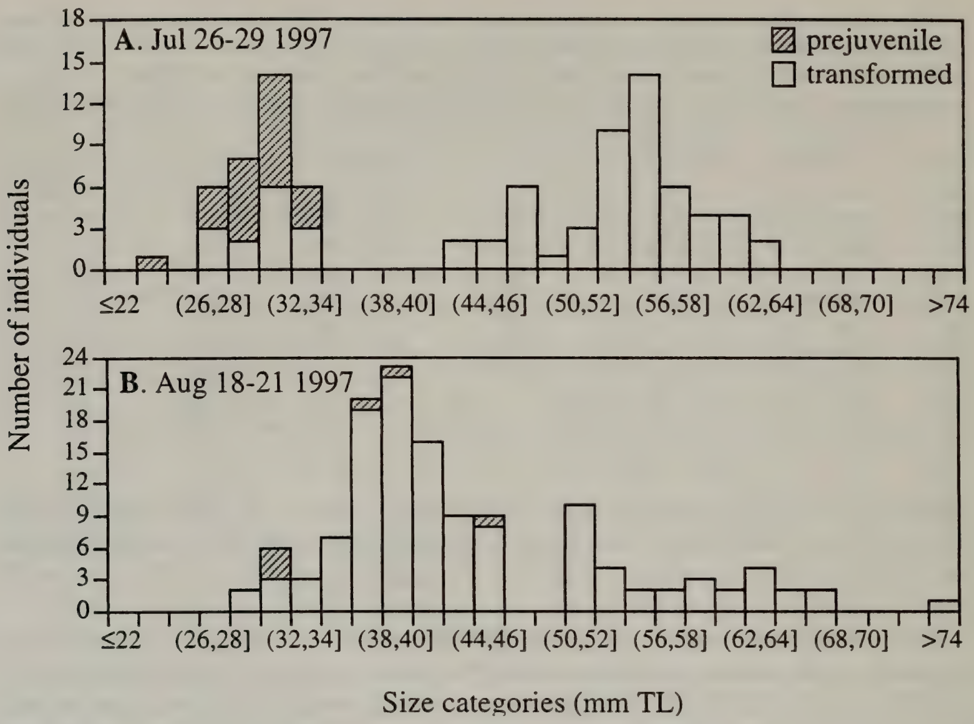


Figure 1. An example of opaleye cohorts distinguishable by size-frequency histograms. Two cohorts settled at Dike Rock during the summer of 1997. The two cohorts A) from July 26 to July 29, 1997, at the end of the settlement period for the smallest cohort, and B) from August 18 to August 21, after three weeks of growth. A few prejuveniles were still contributing to the younger cohort, but most juveniles had already settled.

cohorts. Cohorts recruiting during the El Niño period had higher spot-proportions than those recruiting during non-El Niño periods. Within cohorts, regardless of climate period, the proportion of multi-spotted fish increased over time.

Among-cohort variability.—Increases in the proportion of multi-spotted *Girella* (P_M) among cohorts recruiting during the El Niño period could have resulted from several processes. Environmental disturbance tends to promote marine fish hybridization (Rao and Lakshmi 1999), and the 1997–98 El Niño event may have served as a natural disturbance inducing more interbreeding of *G. nigricans* and *G. simplicidens* in the southern hybrid zone. Northward transport of hybrid larvae to San Diego might have increased during El Niño due to changes in currents. Opaleye larvae are neustonic, usually found up to 110 km from shore (Stevens et al. 1989), and are subjected to surface transport by the southward offshore California Current and the northward inshore California Countercurrent. During the 1997–98 El Niño event, the California Current moved offshore and the California Countercurrent increased in velocity (Norton et al. 1985; Lynn et al. 1998). As a result, the inshore band of northward transport widened, encompassing a greater width of the cross-shore opaleye larval distribution, and the northward transport of anomalously warm water increased (Lynn et al. 1998), presumably along with associated larvae. Hybrid larvae transported north may also have experienced increased survivorship. If hybrids are intermediate between *G. nigricans*

Table 3. Comparison of the proportion of opaleye with three spots (P_3) and four spots (P_4) in each cohort. Cohorts are identified as in Table 1. A paired *t*-test indicates that P_3 is greater than P_4 within cohort ($n = 9$, $t = 2.40$, $p = 0.034$).

Site	Cohort	P_3	P_4
DR	sum 97 1	0.045	0.024
DR	sum 97 2	0.044	0.031
FP	sum 97	0.038	0.006
DR	win 98	0.060	0.089
FP	win 98	0.165	0.096
DR	sum 98 1	0.065	0.053
DR	sum 98 2	0.057	0.021
FP	sum 98	0.035	0.029
DR	sum 99	0.061	0.030

and *G. simplicidens* in temperature-related characters, as they are in spot number, then opaleye with a southern, warm-water *G. simplicidens* ancestor might survive better in warmer El Niño years than colder years.

The multi-spotted fish collected in San Diego may not be hybrid offspring, but instead may reflect a polymorphism for spot number within the San Diego population. In this case, the variable P_M among cohorts may have resulted from temperature-sensitive expression of genes controlling spot number. Although spot number is not a plastic trait after post-settlement development (Orton et al. 1987), conditions during the larval stage may dictate the number of spots that are to develop. Alternatively, larvae with additional-spot alleles may experience different survivorship during different environmental conditions, leading to recruiting cohorts with different spot proportions. If fish with additional spots are characterized by other southern traits, such as higher warm-water affinity, then anomalously warm El Niño events might lead to cohorts with higher P_M. However, in the present study, the response of spot proportion to temperature was not consistent in two ways. First, the two El Niño cohorts recruited during the winter of 1998, which although anomalously warm, was still cooler than the usual summer season of recruitment. The fact that these El Niño cohorts were in addition the only two winter cohorts also complicates the comparison among these and the summer-recruiting normal and La Niño cohorts. Second, La Niña temperature was about 1–2°C cooler than long-term (1966–1994) average temperatures (Davis 2000a), but spot proportions of fish recruiting during early (summer 1998) and late (summer 1999) La Niña conditions were not lower than "normal" period spot proportions (Figure 2).

Within-cohort variability.—The within-cohort variability of P_M observed in the present study is opposite to that expected based on Orton et al. (1987)'s examination of fish size and spot proportion. In the present study, the proportion of multi-spotted fish within most cohorts increased over time as fish grew larger (Figure 3). At one of Orton et al. (1987)'s sites, the proportion of multi-spotted fish was lower in 1–3 year-old fish (>60 mm SL or > about 75 mm TL) than in young-of-the-year fish (30–60 mm SL or about 37–75 mm TL), suggesting that survivorship of fish with extra spots was lower than that of two-spotted fish.

Results of the present study were not consistent with this suggestion. Two explanations may account for the discrepancy. First, Orton et al. (1987) studied

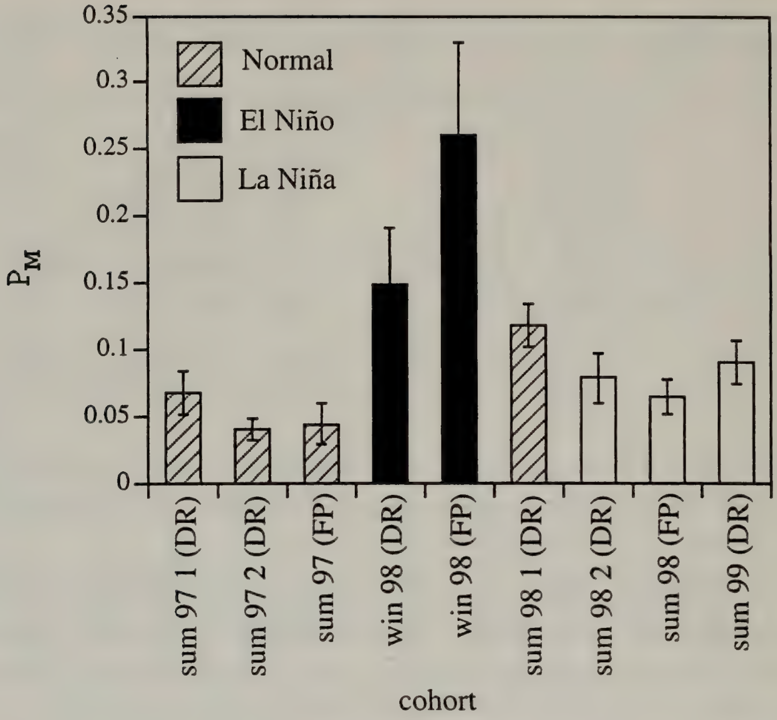


Figure 2. Average weekly proportion of multi spotted opaleye (P_M) ± 1 SE (back-transformed) among nine opaleye cohorts sampled at Dike Rock (DR) and False Point (FP) during normal, El Niño, and La Niña climate periods. Cohorts are named by season, year, order of settlement, and site as in Table 1.

fish from 30–120+ mm SL (about 37–150+ mm TL), and grouped 30–60 mm SL (about 37–75 mm TL) fish for size comparisons. In the present study, most cohorts were not followed beyond 75 mm TL, so the two studies examined slightly different ranges of *G. nigricans'* life history. The proportion of multi-spotted fish may increase during opaleye's intertidal phase (<75 mm TL, Stevens et al. 1989), as indicated by the present study, then decrease after the intertidal phase, as suggested by Orton et al. (1987). Second, in Orton et al. (1987), large and small fish were collected at the same time, so comparisons were made across cohorts. The present study shows that different cohorts can have significantly different proportions of multi-spotted fish. As a result, across-cohort comparisons may not adequately address survivorship or selection issues. Therefore, variability in spot proportion among size classes at a particular time in Orton et al. (1987) might not have been the result of differences in survivorship of multi-spotted fish as a cohort aged, but may reflect variability among cohorts.

The increased frequency of multi-spotted fish over time in most of the cohorts in the present study indicates that within the size range of 30 to 75 mm TL, over the course of several months, the survivorship of multi-spotted fish is higher than that of two-spotted fish. Intertidal opaleye generally occupy middle and upper tidepool habitats (Davis 2000b), which can reach temperatures during spring and summer daytime low tides that are above their preferred temperature of 27–28°C

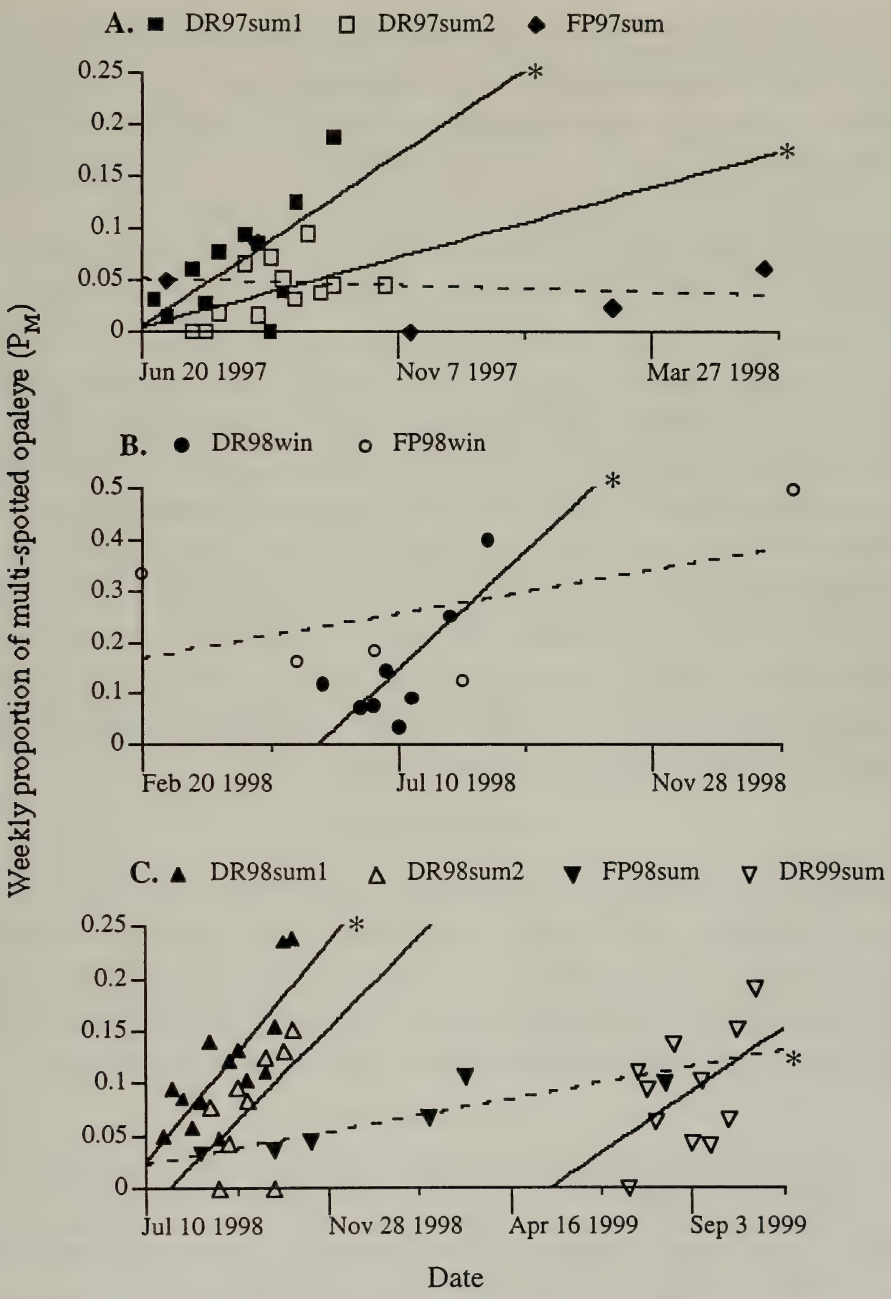


Figure 3. Weekly proportions of multi-spotted opaleye (P_M) over time of each of the nine False Point (FP) and Dike Rock (DR) cohorts. Cohorts are named as in Table 1. A) Cohorts that recruited in the summer of 1997; B) cohorts that recruited in the winter of 1998; C) cohorts that recruited in summer 1998 and summer 1999. Dotted lines and solid lines indicate regression lines for cohorts from FP and DR, respectively. Asterisks indicate regression lines with slopes significantly different from zero. See Table 2 for r^2 and p-values.

(Norris 1963) and close to their lethal maximum temperature (Douderoff 1942). If the presence of additional spots is associated with warm-water adaptations, multi-spotted fish might cope with high temperatures better than two-spotted fish during the intertidal life-history phase. Survivorship of multi-spotted fish in size classes larger than 75 mm TL might then decrease after this intertidal phase during the colder subtidal phase, perhaps explaining why Orton et al. (1987) observed lower proportions of multi-spotted fish in larger size classes.

Conclusion.—The presence of a visible, easily measured hybrid intermediate trait potentially associated with temperature affinity, like dorsal spot pattern in *G. nigricans,* provides an ideal tool with which to measure effects of climate change on gene flow and genetic expression within populations. Further studies are needed to explicitly address selection and survivorship questions. Genetic analysis could establish whether *G. nigricans* and *G. simplicidens* are distinct species and also whether spot number is associated with other warm-water southern or cold-water northern traits. If these are two species, collections over a latitudinal range in southern Baja and the Gulf of California could establish whether stabile hybrid *Girella* populations exist, where the boundaries of the *Girella* hybrid zone are, and the extent to which the two species share genetic information. Tagging studies in which individuals are followed through time would address survivorship questions based on fewer assumptions than cohort analysis. Such information would contribute both to the understanding of influences on hybridization in marine fishes and the sensitivity of hybridization to climate change. Management plans of *Girella* recreational and commercial fisheries would also benefit from information about species identities and hybridization.

Acknowledgments

The field assistance of Doug MacIntyre, Edward Vowles, Andrew Juhl, Erin Hubbard, Nicole Dederick, and Julie Frost is greatly appreciated. Thanks to Lisa Levin, Trevor Price, Dave Checkley, Phil Hastings, Paul Dayton, Paul Smith, and Clint Winant for offering comments on the manuscript. Support was provided by the Department of Defense National Science and Engineering Graduate Fellowship, the J. M. Hepps Graduate Fellowship, Sigma Delta Epsilon Graduate Women in Science, and the Mildred Mathias, Sigma Xi, and PADI Foundations.

Literature Cited

Arntz, W. E. and J. Tarazona. 1990. Effects of El Niño 1982–83 on benthos, fish and fisheries off the South American Pacific coast. Pp. 323–360 *in* Global Ecological Consequences of the 1982–83 El Niño-Southern Oscillation. (P. W. Glynn, ed.), Elsevier Press, xx + 563 pp.

Barry, J. P., C. H. Baxter, R. D. Sagarin, and S. E. Gilman. 1995. Climate-related, long-term faunal changes in a California rocky intertidal community. Science 267: 672–675.

Davis, J. L. D. 2000a. Changes in a tidepool fish assemblage on two scales of environmental variation: season and ENSO. Limnol. Oceanogr. 45: 1368–1379.

Davis, J. L. D. 2000b. Spatial and seasonal patterns of habitat partitioning in a guild of southern California tidepools fishes. Mar. Ecol. Progr. Ser. 196: 253–268.

Douderoff, P. 1942. The resistance and acclimatization of marine fishes to temperature changes I: Experiments with *Girella nigricans* (Ayres). Biol. Bull. 83: 219–244.

Gibson, R. N., L. Pihl, M. T. Burrows, J. Modin, H. Wennhage, and L. A. Nickell. 1998. Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. Mar. Ecol. Progr. Ser. 165: 145–159.

Hubbs, K. 1955. Hybridization between fish species in nature. System. Zool. 4: 1–20.

Lynn, R. J., T. Baumgartner, J. Barcia, C. A. Collins, T. L. Hayward, and others. 1998. The state of the California current, 1997–1998: transition to El Niño conditions. CalCOFI 39: 25–49.

Morris, R. W. 1960. Temperature, salinity, and southern limits of three species of Pacific cottid fishes. Limnol. Oceanogr. 5: 175–179.

Nakamura, R. 1976. Temperature and the vertical distribution of two tidepool fishes. Copeia 1976: 143–152.

Norris, K. S. 1963. The functions of temperature in the ecology of the percoid fish *Girella nigricans* (Ayres). Ecol. Monogr. 33: 23–61.

Norton, J. D., R. McLain, R. Brainard, and D. Husby. 1985. The 1982–83 El Niño event off Baja and Alta California and its ocean climate context. Pp. 44–72 *in* El Niño North: Niño effects in the Eastern Subarctic Pacific Ocean. (W. S. Wooster and D. L. Fluharty, eds.), Washington Sea Grant Program, v + 312 pp.

Orton, R. D., and Buth. 1984. Minimal genetic difference between *Girella nigricans* and *Girella simplicidens*. Isozyme Bull. 17: 66.

Orton, R. D., L. S. Wright, and H. Hess. 1987. Spot polymorphism in *Girella nigricans* (Perciformes: Kyphosidae): geographic and inter-size class variation. Copeia 1987: 198–204.

Rao, K. S. and K. Lakshmi. 1999. Cryptic hybridization in marine fishes: significance of narrow hybrid zones in identifying stable hybrid populations. J. Nat. Hist. 33: 1237–1259.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1991. World fishes important to North Americans, exclusive of species from the continental waters of the United States and Canada. Amer. Fish. Soc. Spec. Publ. 21.

Stevens, E. G., W. Watson, and H. G. Moser. 1989. Development and distribution of larvae and pelagic juveniles of three kyphosid fishes (*Girella nigricans, Medialuna californiensis, and Hermosilla azurea*) off California and Baja California. Fish. Bull. 87: 745–768.

Thomson, D. A., L. T. Findley, and A. N. Kerstitch. 1979. Reef Fishes of the Sea of Cortez: the Rocky-shore Fishes of the Gulf of California. Wiley, xvii + 302 pp.

Zander, C. D., J. Nieder, and K. Martin. 1999. Vertical distribution patterns. Pp. 26–53 *in* Intertidal Fishes. (M. H. Horn, K. L. M. Martin, and M. A. Chotkowski, eds.), Academic Press, xiv + 399 pp.

Accepted for publication 19 June 2000.

Bull. Southern California Acad. Sci.
100(1), 2001, pp. 36–43

Diversity of Parasitic *Cuscuta* and their Host Plant Species in a *Larrea-Atriplex* Ecotone

Simon A. Lei

Department of Biology, Community College of Southern Nevada,
6375 West Charleston Boulevard, WDB, Las Vegas, NV 89146-1139

Abstract.—The distribution of four species of parasitic dodder (*Cuscuta* spp.) on a variety of host plant species was quantitatively investigated in a creosote bush-saltbush (*Larrea tridentata-Atriplex* spp.) ecotone in the Amargosa Valley of southern Nevada. Species of *Cuscuta* did not parasitize all of their potential host plants equally. Although white bursage (*Ambrosia dumosa*) was the most abundant species in the community, *Cuscuta* showed the highest frequency of infestation on *Larrea. Cuscuta* biomass was greatest in *Larrea,* possibly because of *Larrea's* large above-ground canopy. Among the host species, *Larrea* plants exhibited the highest mortality from parasitism. Annuals, biennials, and herbaceous perennials exhibited little or no infestation by *Cuscuta* species. Host plants with heavy infestation showed a significant reduction in survival and flowering success compared to host plants with light or no infestation. Although a generalist in their parasitic nature on a variety of host plant species, different *Cuscuta* species demonstrate specialized opportunistic behavior in their degree of selection and preference for specific individual host species irrespective to host abundance. Two of the primary factors for which different *Cuscuta* species selected their respective hosts were host morphology (lifeform) and phenology (developmental stage).

Parasitism occurs when an association exists between two species that benefits the parasitic organism at the expense of its host organism. The host constitutes a living microhabitat for the parasite. The monotypic family Cuscutaceae has a cosmopolitan occurrence, represented solely by one genus *Cuscuta* (dodder), with many species native to North America (Kuijt 1969). This family is often included as a subfamily of Convolvulaceae, but differs in its parasitic life-form (Kuijt 1969). Species of *Cuscuta* are among the best known of the higher vascular plant parasites because of their extraordinary appearance and behavior (Kuijt 1969).

Multiple species of *Cuscuta* are known to occur in southern Nevada (Cronquist 1984), with different *Cuscuta* species parasitizing different xerophytic and halophytic hosts. *Cuscuta salina* is known to primarily parasitize halophytes, such as four-winged saltbush (*Atriplex canescens*), shadscale (*A. confertifolia*), and iodine bush (*Allenrolfea occidentalis*) (Kearney and Peebles 1951). *Cuscuta californica* occurs frequently on white bursage (*Ambrosia dumosa*) (Beauchamp 1986). Two common host plant species of *Cuscuta denticulata* are creosote bush (*Larrea tridentata*) and cheesebush (*Hymenoclea salsola*) (Beauchamp 1986). Hosts of *Cuscuta campestris* are mostly herbaceous, including composites and grasses (Munz 1974). In an area with multiple species of *Cuscuta,* identifications of these parasites are distinguished primarily by their geographical location, floral morphological characteristics, and by their host plant species (Wesley Niles, personal communication).

Seeds of *Cuscuta* spp. germinate near the soil surface, and may develop a small root system which sustains the plant until the stem reaches a suitable host plant. Many species of *Cuscuta* lack chlorophyll and do not photosynthesize (Belzer 1984). *Cuscuta* spp. have only scale-like vestigial leaves, depending solely on exploitation of resources from their hosts for growth, survival, and regulation of their environment (Whitson 1987). The orange-colored, spaghetti-like parasitic threads function as runners, allowing an individual to move from host to host, as well as to densely infest a single host (Kelly et al. 1988). Upon attachment to a host, a *Cuscuta* plant becomes entirely parasitic, with subsequent degeneration of its terrestrial root system (Kelly 1992), and the resource acquisition is entirely above-ground. A stem of *Cuscuta* spp. infests its host by coiling around the host stem or leaf and sending haustoria into the host's vascular system (Kelly 1992). Soon after the first haustorial contacts have been made, the radicle dies and all contact with the soil is irrevocably lost (Kuijt 1969).

The objective of this study was to examine the distribution of four *Cuscuta* species on 11 host plant species in the Amargosa Valley of southern Nevada. Specifically, woody and subwoody plant species were identified and assessed for 1) *Cuscuta* biomass and relative percent cover of host covered by *Cuscuta* as a measure of the degree of infestation; 2) flowering success between the infested and uninfested host plants; and 3) condition (living or dead) of each infested host individual.

Materials and Methods

Study Site

Field studies were conducted during Spring 1998 in the Amargosa Valley (roughly 36°50′ N, 116°05′ W) of southern Nevada where multiple species of *Cuscuta* were present. The woody vegetation zone (elevation 760 m) was dominated by *Larrea-Atriplex* spp., with numerous individuals of *Ambrosia* and a few individuals of *Hymenoclea,* seepweed (*Suaeda torreyana*), and *Allenrolfea.* A low abundance of annual and perennial herbaceous species was also present, including milkvetch (*Astragalus* spp.), desert marigold (*Baileya pleniradiata*), bugseed (*Dicoria canescens*), desert globemallow (*Sphaeralcea ambigua*), and fluff grass (*Erioneuron pluchellum*).

The Amargosa Valley was selected on the basis of an abundant infestation of *Cuscuta* species in a relatively homogeneous habitat with a variety of host plant species. This area thus provides an assessment of host specialization in four *Cuscuta* species (*C. california, C. campestris, C. denticulata,* and *C. salina*) without having the effects of significantly different environmental variables inherent with the selection of separate geographic study sites.

Field Surveys

Two hectares northeast of U.S. Highway 95 were selected in the Amargosa Valley. Within these two hectares, all plant species were identified, but only woody species abundance (number of individuals) were determined. The amount of host canopies covered with green leaves and covered with their respective *Cuscuta* species, along with the flowering success of host plants were visually

Table 1. Four species of *Cuscuta* parasitizing 11 host species in a *Larrea-Atriplex* ecotone in the Amargosa Valley of southern Nevada. Lifeforms (S = Shrub, Ss = subshrub, A = Annual, B = Biennial, and HP = Herbaceous Perennial) of host plants are shown. Names of host and parasitic species are arranged alphabetically.

Parastic species	Host species	Lifeform
Cuscuta californica	*Ambrosia dumosa*	S
C. campestris	*Baileya pleniradiata*	HP
	Chaenactis fremontii	A
	Oryzopsis hymenoides	HP
C. denticulata	*Hymenoclea salsola*	S
	Larrea tridentata	S
	Sphaeralcea ambigua	HP
C. salina	*Allenrolfea occidentalis*	S
	Atriplex canescens	S
	Atriplex confertifolia	S
	Suaeda torreyana	Ss

estimated in 10-% point increments (Lei 1999a, b, and c). Host plants that lacked flower or fruit production and without green leaves on branches were assumed dead. The condition of seven woody and subwoody (suffrutescent) species covered with parasites was recorded as either live (1) or dead (0). All parasitic stems were collected from all woody and suffrutescent host plants with infestations, and were oven-dried at 45°C for 72 hours in a biology laboratory at the Community College of Southern Nevada (CCSN) to determine biomass accumulation of *Cuscuta.*

Statistical Analyses

One-way Analysis of Variance (ANOVA), followed by Tukey's multiple comparison test were used to detect differences in *Cuscuta* biomass among host species, and to compare means of *Cuscuta* biomass when a significant infestation effect was detected, respectively (Analytical Software 1994). The ANOVA was also employed to detect survival and flowering success between infested and uninfested host individuals. Mean values were presented with standard errors, and statistical significance was determined at $p \leq 0.05$.

Results

Four species of *Cuscuta* were found to primarily parasitize seven woody and subwoody species, as well as two annual and two herbaceous perennial species within the study area (Table 1). Hosts of *C. campestris* were herbaceous plants, including *Baileya* and Indian ricegrass (*Oryziopsis hymenoides*), while hosts of *C. denticulata* were woody plants, such as *Hymenoclea* and *Larrea* (Table 1). Herbaceous plants that were rarely infested with parasites included the annuals *Baileya* and *Chaenactis fremontii,* as well as the perennials *Oryzopsis* and *Sphaeralcea* (Table 2). Conversely, fiddleneck (*Amsinckia tessellata*), Astragalus spp., grama grass (*Bouteloua barbata*), *Dicoria,* and *Erioneuron* revealed no infestation at all (Table 2).

The percentage of host canopies covered by multiple species of *Cuscuta* varied significantly among the host types (Table 1; Fig. 1). Although *Ambrosia* was the

Table 2. Percentage of host canopies (mean ± S.E.) (annuals, biennials, and herbaceous perennials) covered by multiple species of *Cuscuta* in a *Larrea-Atriplex* ecotone in the Amargosa Valley of southern Nevada. Species of *Cuscuta* generally exhibited little or no infestation on herbaceous host plants. Host species names are arranged alphabetically and their lifeforms are shown below. Symbols of host plant lifeforms are explained in Table 1.

Host species	Lifeform	% cover of *Cuscuta* spp.
Amsinckia tessellata	A	Not infested
Aristida glauca	HP	Not infested
Astragalus spp.	HP	Not infested
Baileya pleniradiata	A	9.9 ± 1.3
Bouteloua barbata	A	Not infested
Bromus rubens	A	Not infested
Chaenactis fremontii	A	10.2 ± 2.4
Cirsium neomexicanum	B	Not infested
Cryptantha spp.	A	Not infested
Dicoria canescens	A	Not infested
Erioneuron pluchellum	HP	Not infested
Malacothrix glabrata	A	Not infested
Muhlenbergia porteri	HP	Not infested
Oryzopsis hymenoides	HP	8.3 ± 2.2
Sphaeralcea ambigua	HP	6.7 ± 2.1
Sporobolus cryptandrus	HP	Not infested

most abundant host species, it had a low frequency of *C. californica* infestation. *Larrea* plants were less abundant than *Ambrosia,* yet had the highest frequency of *C. denticulata* infestation (Fig. 1). A significant difference was detected between *Larrea* and *Hymenoclea* in percentage of host canopy cover infested by *C. denticulata* ($P \leq 0.05$; Fig. 1).

Biomass accumulation of *Cuscuta* species also varied significantly ($P \leq 0.001$) among the infested host plant species (Fig. 2). *Larrea* plants had the greatest mean percentage covered by *C. denticulata,* and had the greatest mean *C. denticulata* biomass because of the large above-ground canopy (Fig. 2). *Atriplex* spp. also exhibited abundant *C. salina* biomass on their canopies, whereas other woody taxa contained a relatively low parasitic biomass (Fig. 2). From casual observations, more parasitic biomass was found in the center than around the periphery of shrub canopies. Within the same perennial shrub species, *Cuscuta* revealed the greatest biomass on individual plants that were more vigorous with a rapid growth rate. Host plants not infested with parasites showed a significantly ($P \leq 0.01$; data not shown) greater percentage of green leaves and active flowering than host plants infested with parasites. Hosts with heavy infestation exhibited a significant ($P \leq 0.01$; data not shown) reduction in green leaves and flowering success compared to hosts with light or no infestation.

Condition (survival) of woody and subwoody hosts infested with *Cuscuta* species was observed. *Larrea* and *Atriplex* spp. displayed a greater degree of infestation by *C. denticulata* and *C. salina,* respectively, based on percent cover and biomass than the more abundant *Ambrosia* (Figs. 1–2). Among the woody and subwoody plants, *Larrea* had the highest, while *Allenrolfea* had the lowest number of dead hosts (Fig. 3). Although most host plants were alive, several dead hosts including *Atriplex* spp., *Larrea, Ambrosia,* and *Hymenoclea* with live parasites

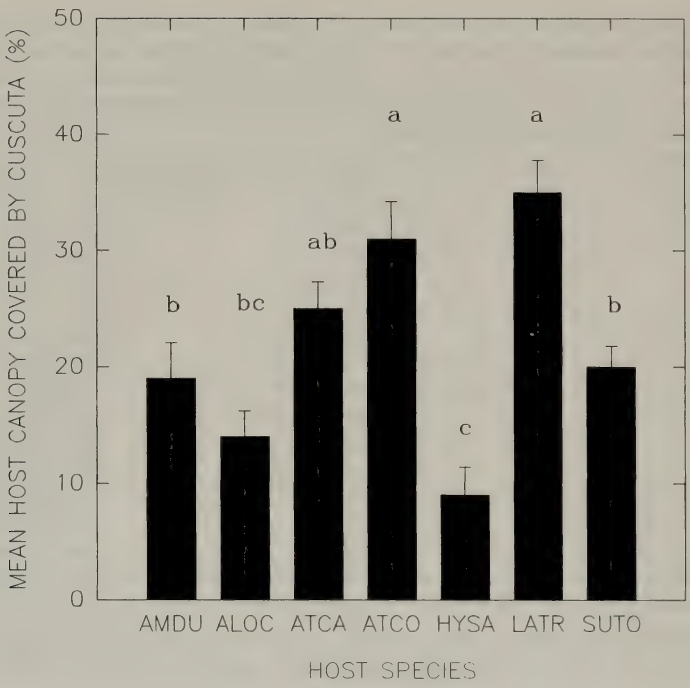


Fig. 1. Percentage of host canopies (mean ± S.E.) covered by multiple species of *Cuscuta* on the seven woody and subwoody host species in a *Larrea-Atriplex* ecotone in the Amargosa Valley of southern Nevada. Only host species infested with *Cuscuta* were computed. Narrow vertical bars denote standard errors of the means. Different letters at the top of columns indicate significant differences at $p \leq 0.05$ using Tukey's Multiple Comparison Test. Host species abbreviations: *Allenrolfea occidentalis* (ALOC), *Ambrosia dumosa* (AMDU), *Atriplex canescens* (ATCA), *Atriplex confertifolia* (ATCO), *Hymenoclea salsola* (HYSA), *Larrea tridentata* (LATR), and *Suaeda torreyana* (SUTO).

were found (Fig. 3). Despite being considered alive, some nearly dead hosts were also found in all seven woody and subwoody species. Within the same host species, significantly greater ($P \leq 0.05$; data not shown) infestation by parasites were observed on individual hosts with greater height and canopy size.

Discussion

In general, *Larrea* plants were the most preferred host, followed by *Atriplex* spp. for the growth of parasites. This study supports the theory that *Cuscuta* spp. are not a strict generalist in the sense that they do not equally infest all available host types in proportion to host abundance. My data reinforces Kelly et al. (1988) study, suggesting that *Cuscuta* species are selective consumers with multiple species of *Cuscuta* parasitizing different species of host plants. Although *Ambrosia* was the most abundant species, *Larrea* exhibited the highest mortality from parasitism in this study.

Kelly (1992) found that *Cuscuta* species made morphological changes gauged towards expected resource (water and nutrient) gain from the host. Species of *Cuscuta* exhibit behavior in which they grow away from host plants with low nutrient availability and rapidly coiled around host plants with high nutritional value (Kelly 1992). Rejection of a potential host indicates that a parasitic plant

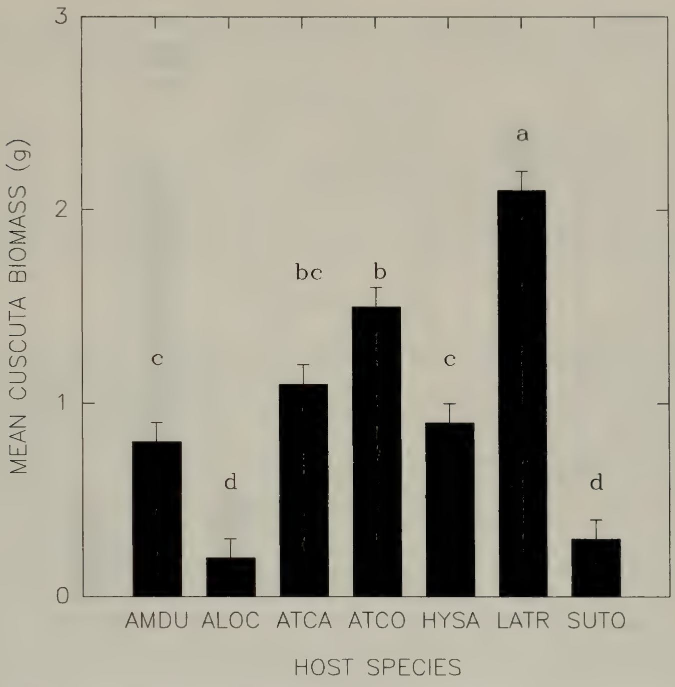


Fig. 2. Biomass of *Cuscuta* species (mean ± S.E.) on the seven woody and subwoody host species in a *Larrea-Atriplex* ecotone in the Amargosa Valley of southern Nevada. Only host species infested with *Cuscuta* were computed. Narrow vertical bars denote standard errors of the means. Different letters at the top of columns indicate significant differences at $p \leq 0.05$ using Tukey's Multiple Comparison Test. Host species abbreviations are explained in Figure 1.

may strategically take the risk of forfeiting the initial host for the chance of acquiring better resources from another host later (Kelly 1992).

There are several potential explanations for the dispersal of *Cuscuta* seeds. First, the seeds of *Cuscuta* species appear to be dispersed haphazardly; animals as dispersal agents are probably rare and unimportant (Kuijt 1969). Second, some *Cuscuta* seeds may fall to the ground and germinate there. Third, seeds of *Cuscuta* may be transported by wind or water to new hosts (Kuijt 1969). Fourth, the reason why some *Cuscuta* species infested more than others is not completely known. It may be a maternal influence when *C. denticulata* seedlings from plants grown on *Larrea* select *Larrea* more often than *Cuscuta* spp. seedlings from other host species. Consequently, the emerging *C. denticulata* seedlings would grow directly and lead to a more vigorous growth on the *Larrea* plants. Although a number of annual and perennial herbaceous species were not infested by parasites, these species were potential hosts because they were present in the community.

Biomass accumulation of *Cuscuta* species differed significantly among host species. Woody perennials showed the greatest *Cuscuta* biomass, whereas annuals, biennials, and herbaceous perennials exhibited minimal or no infestations in this study. A limited *Cuscuta* infection success on biennials and herbaceous perennial hosts is related to host morphology (lifeform) since the presence of scattered vascular bundles in grasses may not be amenable to resource exploitation by *Cuscuta* species (Kelly and others 1988). Additionally, host phenology (devel-

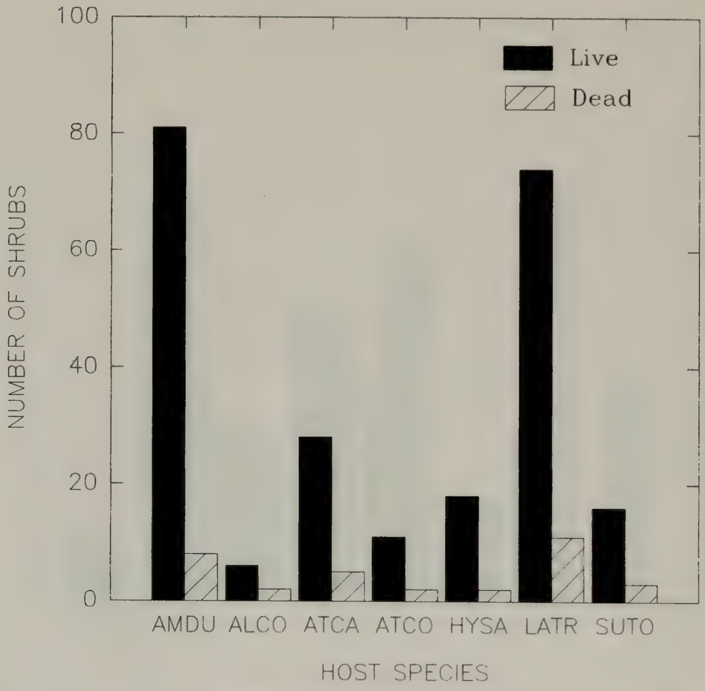


Fig. 3. Condition (live or dead) of the seven woody and subwoody host species infested with *Cuscuta* species in a *Larrea-Atriplex* ecotone in the Amargosa Valley of southern Nevada. Host species abbreviations are explained in Figure 1.

opmental stage) is also likely to determine the biomass and abundance of *Cuscuta* species. Mature or long-lived plants generally have a greater canopy size compared with juvenile or short-lived plants. Within the same host species, a relatively large host canopy size would indicate a greater surface area available on secondary branches for successful colonization and establishment of *Cuscuta* species. In this study, *Cuscuta* accumulated more tissue or biomass on those hosts that grew better and faster, presumably due to higher moisture content and nutritional value. Not all xerophytic plants functioned equally as hosts for multiple species of *Cuscuta* in this study. Although water and nutrient availability were not quantitatively examined, infection of parasite on the host, as demonstrated by the higher probability of infestation on *Larrea* and *Atriplex* spp. in comparison to *Ambrosia,* may be attributed to proportionally different water and nutrient uptake by these host plant species, or to different characteristics of the hosts and/or parasitic species.

Host morphology and phenology were two main factors that partially determined which species of *Cuscuta* parasitizing which species of host plants. Within the same host species in this study, species of *Cuscuta* tended to select individual hosts with greater height and canopy size. Seedlings appear to grow toward a source of high nutrient and, to a lesser extent, moisture (Kuijt 1969). Host morphology and phenology may be strongly associated with the availability of water and nutrients. Host preference in multiple species of *Cuscuta* are still not fully understood. Further research, including water and nutrient status of existing and potential host plants, at various geographical locations, are required to improve our understanding regarding the host preference in parasitic *Cuscuta* plants.

Acknowledgments

Valuable field assistance provided by Steven Lei, David Valenzuela, and Shevaun Valenzuela was gratefully acknowledged. Helpful comments by David Charlet greatly improved the manuscript. The Department of Biology at the Community College of Southern Nevada (CCSN) provided logistical support.

Literature Cited

Analytical Software. 1994. Statistix 4.1, an interactive statistical analysis program for microcomputers. Analytical Software, St. Paul, Minnesota. 329 pp.

Beauchamp, R. M. 1986. A Flora of San Diego County, California. Sweetwater River Press, National City, California. 241 pp.

Belzer, T. J. 1984. Road side plants of southern California. Mountain Press Publishing Company, Missoula, Montana. 158 pp.

Cronquist, A. 1984. Intermountain Flora: Vascular Plants of the Intermountain West, The New York Botanical Garden, New York.

Kearney, T. H. and R. H. Peebles. 1951. The Flora of Arizona. University of California Press, Berkeley, California.

Kelly, C. K., D. L. Venable, and K. Zimmer. 1988. Host specialization in *Cuscuta costariensis*: an assessment of host use relative to host availability. Oikos 53:315-320.

Kelly, C. K. 1992. Resource choice in *Cuscuta europaea*. Proc. Nat. Acad. Sci. 89:12194–12197.

Kuijt, J. 1969. The Biology of Parasitic Flowering Plants. University of California Press, Berkeley, California. 246 pp.

Lei, S. A. 1999a. Host-parasite relationship between Utah juniper and juniper mistletoe in the Spring Mountains of southern Nevada. Pages 99–104 in Proceedings: Ecology and management of pinyon-juniper communities within the interior west. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah.

———. 1999b. Phenological events and litterfall dynamics of blackbrush in southern Nevada. Pages 113–118 in Proceedings: Shrubland ecotones. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah.

———. 1999c. Effects of severe drought on biodiversity and productivity in a creosote bush-blackbrush ecotone of southern Nevada. Pages 217–221 in Proceedings: Shrubland ecotones. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah.

Munz, P. A. 1974. A Flora of Southern California. University of California Press, Berkeley, California. 1086 pp.

Whitson, T. D. 1987. The Weeds and Poisonous Plants of Wyoming and Utah. Cooperative Extension Service, Laramie, Wyoming.

Accepted For Publication 19 June 2000

Bull. Southern California Acad. Sci.
100(1), 2001, pp. 44–50

Persistence of the Nematode, *Oswaldocruzia pipiens* (Molineidae), in the Pacific Treefrog, *Hyla regilla* (Hylidae), from California

Stephen R. Goldberg[1] and Charles R. Bursey[2]

[1]*Department of Biology, Whittier College, Whittier, California 90608*
[2]*Department of Biology, Pennsylvania State University, Shenango Campus,*
147 Shenango Avenue, Sharon, Pennsylvania 16146

Abstract.—Multi-year samples of *Hyla regilla* from three California counties (Los Angeles, Orange, Riverside) as well as single-year samples from three additional California counties (Humboldt, Imperial, Santa Clara) were examined for helminths. Gravid individuals of one species of cestode, *Distoichometra bufonis* and two species of nematodes, *Oswaldocruzia pipiens* and *Rhabdias ranae* were found. Metacercariae of two species of trematodes, *Alaria* sp. and *Clinostomum* sp. and larvae of one nematode species, *Physaloptera* sp. were also found. Of the helminths found in the multi-year samples, only *O. pipiens* was persistent; however, it was not stable.

Although many amphibians species have been recorded as hosts for helminth parasites (Prudhoe and Bray 1982; Baker 1987), the majority of this work has concentrated on faunistic surveys typically based upon collections taken during a single season. A general conclusion drawn from these studies is that helminth communities of anurans are depauperate and isolationist in character (Barton 1997). However, two measures of helminth communities developed by Meffe and Minckley (1987) are not addressed in these single season collections: persistence, a measure of presence or absence of a species over time, and stability, a qualitative measure based upon the relative constancy of species abundances over time. These measures can only be addressed with long-term studies; unfortunately, there are few published accounts of long-term variation (biennial or greater) in helminth infracommunities of anurans. In Poland, Grossman and Sandner (1953), in Russia, Markov and Rogoza (1949, 1953), and in England, Lees (1962) published data on seasonal variation in the prevalence of helminths of *Rana temporaria.* Also from Poland, Kuc and Sulgostowska (1988) published data collected from *Rana ridibunda* over a period of four years.

The Pacific treefrog, *Hyla regilla* (Baird and Girard 1852), is a small anuran that occurs from British Columbia to the tip of Baja California Sur, México and east to western Montana and eastern Nevada (Stebbins 1985). Pacific treefrogs prefer low plant growth near water and frequent a variety of habitats from sea level to elevations of 3540 m including grassland, chaparral, woodland, forest, desert oasis and farmland (Stebbins 1985). There are seven reports of helminths from northern populations of this frog (Millzner 1924; Douglas 1958; Lehmann 1965; Macy 1960; Efford and Tsumura 1969; Brooks 1976, Johnson et al. 1999) and one report from southern California (Koller and Gaudin 1977).

Multi-year collections of *H. regilla* from three California counties (Los Angeles, Orange, Riverside) as well as single season collections from three California

Table 1. Number (N), SVL, and collection dates of *Hyla regilla* from California counties with number infected by and prevalence (%) of anuran parasites.

County	N	SVL ± SD range (mm)	Collection dates	*Distoichometra bufonis*	*Oswaldocruzia pipiens*	*Rhabdias ranae*
Humboldt	3	39 ± 1.5, 38–41	1997, Aug	—	—	—
Santa Clara	18	34 ± 4.1, 21–40	1998, Jan–May	2 (11)	3 (17)	—
Imperial	2	31 ± 1.4, 30–32	1959, Mar	—	2 (100)	—
Los Angeles	14	30 ± 4.3, 19–35	1943, Mar	—	3 (21)	—
	2	30 ± 0, 30	1944, Mar	—	—	—
	1	25	1963, Mar	—	—	—
	17	30 ± 3.7, 25–36	1971, Jan–Apr	—	7 (41)	—
	2	34 ± 5.0, 30–37	1972, Apr	—	2 (100)	—
Orange	12	35 ± 5.0, 30–48	1957, Feb–Mar	—	—	—
	10	33 ± 4.8, 27–43	1958, Feb	—	—	—
	5	33 ± 7.2, 24–41	1961, Feb	—	1 (20)	—
	4	37 ± 5.0, 30–41	1962, Mar	—	—	—
	8	33 ± 4.4, 29–40	1963, Feb	—	—	—
	2	32 ± 1.4, 31–33	1964, Feb	—	—	—
	2	34 ± 5.7, 30–38	1965, May–Jun	—	—	—
	8	36 ± 2.6, 32–39	1966, Mar	—	1 (13)	—
	2	34 ± 5.0, 31–38	1967, Mar–May	—	1 (50)	1 (50)
	8	29 ± 3.3, 24–35	1972, Feb	—	1 (13)	—
Riverside	1	35	1965, June	—	1 (100)	—
	1	24	1967, May	—	—	—
	3	26 ± 5.0, 21–31	1969, July	—	2 (67)	1 (33)
	1	18	1972, Aug	—	—	—

counties (Humboldt, Imperial, Santa Clara) were examined for helminths. The purpose of this paper is to evaluate persistence and stability of helminths harbored by *H. regilla* from California.

Materials and Methods

One hundred twenty-eight *H. regilla* (mean ± 1 SD snout-vent length [SVL] = 32 mm ± 5 SD, range 18–48 mm) from 6 counties in California were examined (collection data by year is given in Table 1). There were 47 female (SVL = 33 mm ± 6 SD, range = 18–43 mm) and 81 male (SVL = 32 mm ± 4 SD, range = 19–48 mm) frogs in the total sample. All frogs had been fixed in 10% formalin and preserved in 50% ethanol. The body cavity of each frog was opened by a longitudinal incision and the gastrointestinal tract was removed and slit longitudinally. The esophagus, stomach, small intestine, large intestine, lung, urinary bladder, coelom and liver were searched with a dissecting microscope for helminths. Helminths were placed in a drop of undiluted glycerol on a glass slide and allowed to clear for study with a compound microscope. Nematodes were identified from these slides. Cestodes and trematodes were stained in hematoxylin and mounted in balsam for identification. Where applicable, difference in prevalence between male and female frogs was examined by the chi-square test (χ^2), numbers of helminths per male and female hosts were evaluated by the Kruskal Wallis test, and correlation analysis (*r*) was used to relate intensity of infection to age (as estimated by SVL).

Results

Gravid individuals of one species of cestode, *Distoichometra bufonis* Dickey 1921; and two species of nematodes, Oswaldocruzia pipiens Walton 1929, and *Rhabdias ranae* Walton 1929 were found. Metacercariae of two species of trematodes, *Alaria* sp. and *Clinostomum* sp., and larvae of one species of nematode, *Physaloptera* sp., were also found. Only *Oswaldocruzia pipiens* was found to be persistent (Table 1). Number, prevalence (number of infected hosts divided by number of hosts examined), and abundance (number of individuals of a parasite species divided by the number of hosts examined) for each helminth species by locality are given in Table 2. Voucher specimens were placed in vials of 70% ethanol and deposited in the U.S. National Parasite Collection (USNPC): *Alaria* sp. (mesocercaria), 88611; *Clinostomum* sp. (metacercaria), 88612; *Distoichometra bufonis,* 88614; *Oswaldocruzia pipiens,* 88615; *Rhabdias ranae,* 88609; *Physaloptera* sp. (larvae), 88610.

Thirty four frogs (27%) were found to harbor 157 helminths ($\bar{x} = 5 \pm 5$ SD per infected frog). Of these, 29 were larvae of helminth species not capable of completing their life cycles in anurans. Mean helminth species richness for infected frogs was 1.0 ± 0.2 SD, range = 1–2 species. Eighteen of 81 male frogs (22%) harbored 59 helminths; 16 of 47 female frogs (34%) harbored 98 helminths. Prevalence of helminth infection ($\chi^2 = 2.13$, 1 df, $P > 0.05$) as well as number of helminths harbored per host (Kruskal Wallis test = 2.6, 1 df, $P > 0.05$) was not significantly different between male and female frogs. Thirty three frogs (26%) harbored a single species of helminth; 1 frog (1%) harbored 2 species. The smallest infected frog was 26 mm SVL. There was no correlation between number of helminths and SVL ($r = 0.002$, $p > 0.05$). Inspection of Table 2 will show that in no two localities did *H. regilla* harbor the same combination of helminth species and that the helminths preferred specific host locations. This is the first report of metacercariae of *Clinostomum* sp. and larvae of *Physaloptera* sp. in *Hyla regilla.*

Discussion

Barton (1997) described anuran helminth communities as depauperate and isolationist. Depauperate is used in the sense that few helminth species are found in a host species from a particular locality. Table 2 supports the use of depauperate to describe helminth communities harbored by *H. regilla.* Isolationist is used in the sense that helminth density is low, helminth species are unaffected by one another and some niches are absent. Table 2 also supports the use of isolationist to describe helminth communities of *H. regilla.* In addition, none of the helminth species found in this study was unique to *H. regilla.* Of the six helminth species present, *Alaria* sp., *Clinostomum* sp., and *Physaloptera* sp. are incapable of completing their life cycles in anurans. Species of *Alaria* utilize mammals as final hosts and species of *Clinostomum* utilize birds as final hosts; metacercariae of both are commonly found in frogs (Smyth and Smyth 1980). Larvae, but no adults, of *Physaloptera* sp. have been reported from anurans (Anderson 1992). *Distoichometra bufonis* and *Rhabdias ranae* are common parasites of anurans (Brooks 1976; Baker 1987). *Oswaldocruzia pipiens* has been reported from frogs, toads, salamanders, lizards and turtles (Baker 1987). The term generalist should

Table 2. Number (N), prevalence as % (P), abundance (A) and host site of helminths from *Hyla regilla* by California county (north to south).

Helminth	Humboldt			Santa Clara			Los Angeles			Orange			Riverside			Imperial		
Host site	N	P	A	N	P	A	N	P	A	N	P	A	N	P	A	N	P	A
Trematoda																		
Alaria sp. (metacercaria)	—	—	—	3	5	0.2	—	—	—	—	—	—	—	—	—	—	—	—
cysts in skeletal muscle																		
Clinostomum sp. (metacercaria)	2	33	0.7	13	5	0.7	—	—	—	—	—	—	—	—	—	—	—	—
cysts in mesentery																		
Cestoda																		
Distoichometra bufonis	—	—	—	11	11	0.6	—	—	—	—	—	—	—	—	—	—	—	—
small intestine																		
Nematoda																		
Oswaldocruzia pipiens	—	—	—	3	17	0.2	72	33	2.0	16	6	0.3	15	50	2.5	5	100	2.5
small intestine																		
Physaloptera sp. (larvae)	—	—	—	—	—	—	—	—	—	3	3	0.1	—	—	—	—	—	—
stomach																		
Rhabdias ranae	—	—	—	—	—	—	—	—	—	10	5	0.2	1	17	0.2	—	—	—
lungs																		

Table 3. Reports of *Distoichometra bufonis, Oswaldocruzia pipiens* and *Rhabdias ranae* from California by County.

Helminth Host	County	Prevalence (%)	Reference
Distoichometra bufonis			
Bufo boreas	Los Angeles	19/255 (7)	Koller and Gaudin 1977
	Los Angeles	4/69 (6)	Goldberg et al. 1999
Hyla regilla	Los Angeles	2/232 (1)	Koller and Gaudin 1977
	Santa Clara	2/18 (11)	this study
Oswaldocruzia pipiens			
Bufo boreas	Butte	not stated	Ingles 1936
	Kern	not stated	Ingles 1936
	Los Angeles	119/255 (47)	Koller and Gaudin 1977
	Los Angeles	10/30 (33)	Goldberg et al. 1999
	Riverside	1/11 (9)	Goldberg et al. 1999
	San Diego	not stated	Ingles 1936
Hyla regilla	Imperial	2/2 (100)	this study
	Los Angeles	161/232 (69)	Koller and Gaudin 1977
	Los Angeles	12/36 (33)	this study
	Orange	4/61 (7)	this study
	Riverside	3/6 (50)	this study
	Santa Clara	3/18 (17)	this study
Rana aurora	Butte	not stated	Ingles 1936
	Kern	not stated	Ingles 1936
	San Diego	not stated	Ingles 1936
Aneides lugubris	not stated	21/31 (68)	Goldberg et al. 1998
Elgaria multicarinata	Los Angeles	2/96 (2)	Goldberg and Bursey 1990
Rhabdias ranae			
Hyla regilla	Los Angeles	28/232 (12)	Koller and Gaudin 1977
	Orange	1/61 (2)	this study
	Riverside	1/6 (17)	this study
Rana boylii	not stated	not stated	Ingles 1936
	Marin/Sonoma	2/11 (18)	Lehmann 1965

also be used as a descriptor of the helminth communities of *H. regilla* (Table 2). Thus, in each county studied, *H. regilla* harbors a depauperate, isolationist community composed of generalist helminths.

More importantly, data from Los Angeles and Orange Counties (Table 1) suggest that none of these species of helminths maintains a stable population in *H. regilla* and that only *O. pipiens* is persistent, present some years with widely differing prevalences and absent other years. Several questions arise, namely, is absence of a helminth species an artifact of sample size, is *H. regilla* an atypical host, and do stable populations of these helminths exist in these localities? The first question cannot be answered by the data examined; it could only be determined by a long-term study utilizing a large number of hosts. Others have reported these helminths from *H. regilla* (Table 3), thus *H. regilla* is a suitable host. The life cycle of *D. bufonis* is unknown but Joyeux (1927) regards the life history of nematotaeniid cestodes to be direct, that is, without an intermediate host; infection of a new host occurs through ingestion of cestode eggs. Both *O. pipiens* and *R. ranae* have direct life cycles and infection occurs by integumental penetration (Anderson 1992). These three helminths are generalists in that they are capable of infecting a number of hosts (Brooks 1976; Baker 1987). Table 3 lists California records of these three species; however, long-term studies are not available to test stability in these hosts. The advantage to generalist helminths is that a particular host is unimportant; infection in a particular host may fluctuate (Table 3), but the helminth population maintains an overall density.

The conclusion that we draw is that a generalist helminth population may vary drastically within a particular host over time, but within its population of hosts, the helminth species is persistent and most likely stable.

Acknowledgments

We thank R. L. Bezy for the opportunity to examine *H. regilla* from the Natural History Museum of Los Angeles County (Imperial, Los Angeles, Orange, Riverside Counties) and P. T. J. Johnson for treefrogs from Humboldt and Santa Clara Counties.

Literature Cited

Anderson, R. C. 1992. Nematode Parasites of Vertebrates: Their Development and Transmission. CAB International, Wallingford, Oxon, U.K. xii + 578 pp.

Baker, M. R. 1987. Synopsis of the Nematoda parasitic in amphibians and reptiles. Occas. Pap. Biol., Mem. Univ. Newfoundland, 11:1–325.

Barton, D. P. 1997. Why are amphibian helminth communities depauperate? Mem. Mus. Vict., 56: 581–586.

Brooks, D. R. 1976. Parasites of amphibians of the Great Plains. Part 2. Platyhelminths of amphibians in Nebraska. Bull. Univ. Nebraska St. Mus., 10:65–92.

Douglas, L. T. 1958. The taxonomy of nematotaeniid cestodes. J. Parasitol., 44:261–273.

Efford, I. E., and K. Tsumura. 1969. Observations on the biology of the trematode *Megalodiscus microphagus* in amphibians from Marion Lake, British Columbia. Amer. Midl. Nat. 82:197–203.

Goldberg, S. R., and C. R. Bursey. 1990. Helminths of the San Diego alligator lizard, (*Gerrhonotus multicarinatus webbi*) (Anguidae). J. Wild. Dis., 26:297–298.

———, ———, and H. Cheam. 1998. Composition and structure of helminth communities of the salamanders, *Aneides lugubris, Batrachoseps nigriventris, Ensatina eschscholtzii* (Plethodontidae), and *Taricha torosa* (Salamandridae) from California. J. Parasitol., 84:248–251.

———, ———, and S. Hernandez. 1999. Helminths of the western toad, *Bufo boreas* (Bufonidae) from southern California. Bull. S. Cal. Acad. Sci., 98: 39–44.

Grossman, T., and H. Sandner. 1953. Helmintofauna plazów Bialowieskiego Parku Narodowego. Acta Parasitol. Polonica, 1:345–352.

Ingles, L. G. 1936. Worm parasites of California amphibia. Trans. Amer. Microsc. Soc., 55:73–92.

Johnson, P. T. J., K. B. Lunde, E. G. Ritchie, and A. E. Launer. 1999. The effect of trematode infection on amphibian limb development and survivorship. Science 284:802–804.

Joyeux, C. 1927. Recherches sur la faune helminthologique Algérienne (cestodes et trématodes). Archs. Inst. Pasteur Alger., 5:509–528.

Koller, R. L., and A. J. Gaudin. 1977. An analysis of helminth infections in *Bufo boreas* (Amphibia: Bufonidae) and *Hyla regilla* (Amphibia: Hylidae) in southern California. Southwest. Nat., 21: 503–509.

Kuc, I., and T. Sulgostowska. 1988. Helminth fauna of *Rana ridibunda* Pallas, 1771 from Goclawski Canal in Warszawa (Poland). Acta Parasitol. Polonica, 33:101–105.

Lees, E. 1962. The incidence of helminth parasites in a particular frog population. Parasitology, 52: 95–102.

Lehmann, D. L. 1965. Intestinal parasites of northwestern amphibians. Yearbook Amer. Philosoph. Soc. pp 284–285.

Macy, R. W. 1960. On the life cycle of *Megalodiscus microphagus* Ingles (Trematoda: Paramphistomatidae). J. Parasitol., 46:662.

Markov, G. S., and M. L. Rogoza. 1949. Parasitic fauna of male and female grass frogs. C. R. Acad. Sci. U.R.S.S. 65:417–420. [in Russian].

———, and ———. 1953. Seasonal and microzonal differences in the parasitic fauna of grass frogs. C.R. Academy of Sciences U.R.S.S. 91:169–172. [in Russian].

Meffe, G. K., and W. L. Minckley. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. Am. Midl. Nat., 117:177–191.

Millzner, R. 1924. A larval acanthocephalid, *Centrorhynchus californicus* sp. nov., from the mesentery of *Hyla regilla.* Univ. Calif. Publ. Zool., 26:225–227.

Prudhoe, S., and R. A. Bray. 1982. Platyhelminth parasites of the Amphibia. British Museum (Natural History) and Oxford University Press, Oxford, 217 pp. + 4 microfiche.

Smyth, J. D., and M. M. Smyth. 1980. Frogs as host-parasite systems I. The Macmillan Press Ltd., London, ix + 112 pp.

Stebbins, R. C. 1985. A field guide to western reptiles and amphibians. Houghton Mifflin Company, Boston, xiv + 336 pp.

Accepted for publication 13 January 2000.

Bull. Southern California Acad. Sci.
100(1), 2001, pp. 51–58

Cercarial Emergence from Rediae in California Snail Tissues

Mark Armitage, M.S.

Azusa Pacific University, P.O. Box 7000/Mary Hill 101, Azusa,
California 91702-7000, 626-815-6000, X5519, marmitage@apunet.apu.edu

Abstract.—Rediae from *Cerithidea californica* snails collected at Point Mugu, CA, yield pleurolophocercous, furcocercous, and xiphidio cercariae. Pleurolophocercous and xiphidio cercariae emerge one at a time from rediae and never tail first. Furcocercous cercariae, on the other hand emerge in multiple numbers and either tail or head first. The pleurolophocercous cercariae collected in this study probably represent either *Ascocotyle sexidigita,* or *A. (Phagicola) diminuta,* both of which have been excysted from metacercarial cysts in *Fundulus parvipinnis* collected at the same site.

Previous authors have described California cercariae which differ from those found at the Point Mugu site. Maxon and Pequegnat (1949) reported that *C. californica* collected from mud flats at upper Newport Bay (CA) yielded 7 different types of cercariae when isolated in incubated finger bowls, including pleurolophocercous (single tail with fin folds), furcocercous (forked tail), and xiphidio (single tail, no fin folds) cercariae which were also found in this study. These authors described one furcocercous, two pleurolophocercous, and three echinostome cercariae, all of which had oral spines or other characteristics unlike those encountered in this study at Point Mugu. Martin (1950a), described the cercariae of *Euhaplorchis californiensis* shed by *C. californica* at Playa del Rey, CA as a parapleurolophocercous type with an oral sucker surrounded by a crown "having four or five short spines in its dorsal part." Martin (1950b) reported cercariae of *Parastictodora hancocki,* also shed by *Cerithidea,* as having three rows of 5–6 spines. Additionally, Martin (1951) described *Pygidiopsoides spindalis* adults experimentally derived from the feeding of infected *F. parvipinnis* specimens to cats and newly hatched chicks, but did not describe the cercariae from this trematode until later (Martin 1964), when he reported that the cercariae, also shed from *Cerithidea* had "oral suckers[s]. . . surrounded by a ring of fourteen large spines." Martin made no descriptions of cercariae in a study of seasonal infections of *Cerithidea* over a one-year period (1955), but Martin (1972) did provide an annotated key to the cercariae that develop in *Cerithidea* from Southern California. Finally, Font, et al. (1984) described the cercaria of a sibling species of *A. sexidigita,* named *A. gemina* from Louisiana and Mississippi, (although *A. gemina* cercariae do not infect *F. parvipinnis*). There were also morphological differences between cercariae of *A. gemina* which had spines and bristles and those cercariae studied here which did not have any of the spines and bristles described by these other authors.

Materials and Methods

Fifty *Cerithidea californica* were hand-collected from the exposed mud flats at low tide at the Laguna Road bridge over the western Mugu lagoon area of the

Point Mugu Naval Air Weapons Station, CA, in May 1999. Algae were also taken from the site. Snails were isolated in 4″ fingerbowls in 12% saline under bright fiber optic illuminators for a period of 36 hours with small quantities of algae. Light cycle illumination was on ten hours per day, followed by a fourteen-hour period of darkness. Snails that yielded cercariae after 36 hours were placed in fresh saline and free swimming cercariae were removed by pipette into fixative. Those snails which did not produce cercariae were placed into fingerbowls for further observation, and were reisolated if cercariae began to emerge. After a week, snails known to yield cercariae were sacrificed by crushing and the tissues, as well as individual cercariae and rediae, were fixed in 2% glutaraldehyde, buffered in .2M sodium cacodylate, postfixed in 2% osmium, and rinsed in water. These were then dehydrated through a graded series of acetone. Cercariae and snail tissue for SEM were air dried, affixed to stubs, coated in gold for 90 seconds, and imaged and photographed on a Jeol SEM at 15 Kv.

Results

Both large and small rediae were observed at times infecting the same *Cerithidea* digestive gland tissues. Most often, however, snails contained only large or only small rediae (FIG 2, 7). Thirty one percent of the collected snails when crushed, yielded rediae in large numbers, infecting only the digestive organs. Four distinct cercariae were shed.

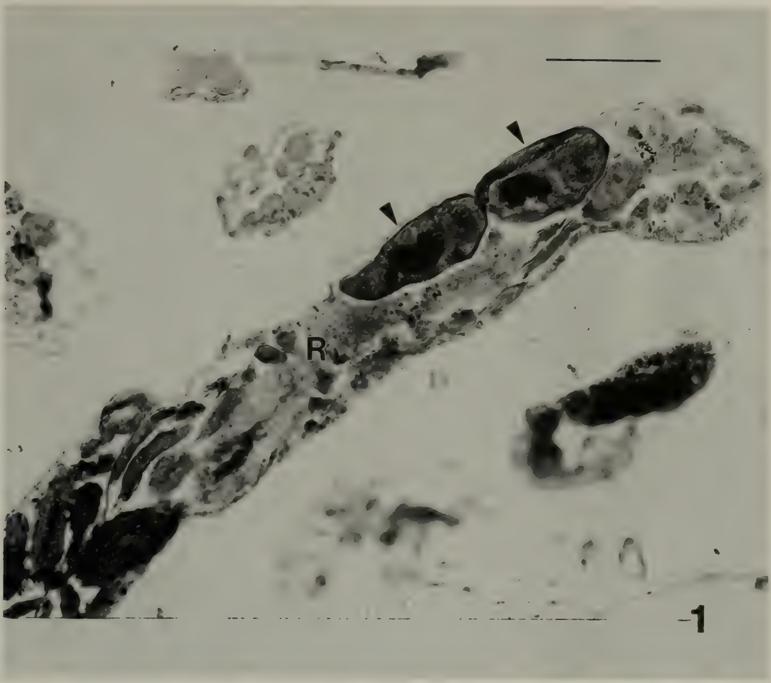
1) One very small xiphidio cercaria, which came out in small numbers, did not dehydrate well and was unsuitable for processing in electron microscopy.

2) The pleurolophocercous cercariae were birthed singly, always head first from rediae which were 275μm thick, 700μm long, and which had unusually large, thickly collared birth pores (FIG 2,3,4). The cercariae have a well-developed oral sucker and a massive ventral sucker ringed by a muscular annulus. Additionally, paired sets of papillae appear on the surface of the cercarial tegument, distal to the oral sucker (FIG 9). A large range in shape and length variability exists in live cercariae (FIG 10), therefore, anatomical features in fixed worms must be considered in light of possible fixation artifacts, including the possible loss of bristles and spines. Although they do have eyespots, no spines were observed on any of the pleurolophocercous cercariae, therefore it is possible that these may represent the larval stage of either *Ascocotyle sexidigita* or of *A. (Phagicola) diminuta,* both of which have been excysted previously from naturally occurring infections in *F. parvipinnis* at the same site (Armitage 1997, 1999).

3) The furcocercous cercariae were birthed from rediae that were 80μm by 450μm and had a single smaller pore (FIG 7), and either came out head or tail first, but were mostly birthed in multiples (FIG 5,6,7). The cercariae came out in such large numbers that the water in the 4″ bowls became a milky white after 10 hours in light. These cercariae do not correspond to any of the descriptions in the literature, as they have an almost cylindrical body shape, no eyespots, and no collar spines.

4) A few furcocercous types resembling those described by Maxon and Pequegnat (1949) were observed (FIG 11), but there were not enough specimens for electron microscopy.

That only 4 types of cercariae were isolated from the site fits well with data previously reported showing the presence of *Pygidiopsoides spindalis, Ascocotyle*



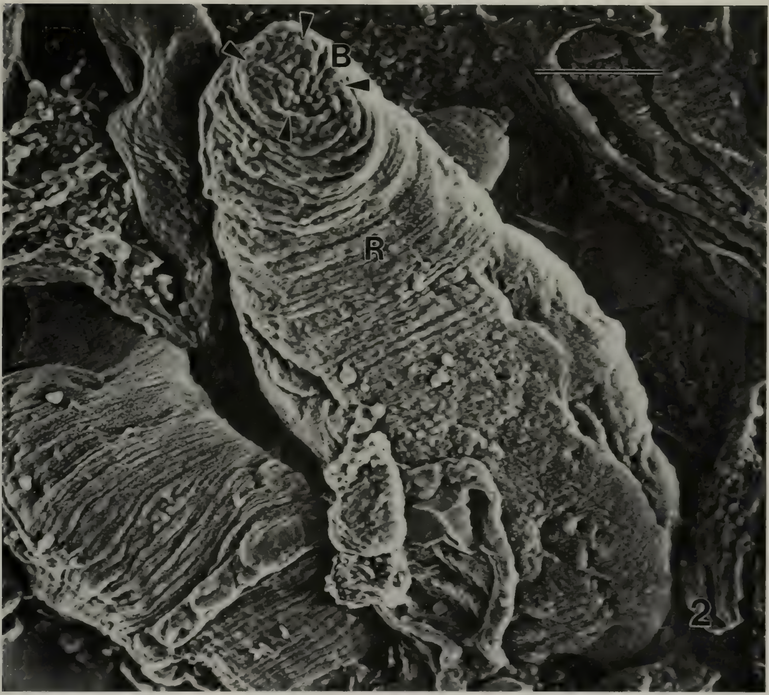
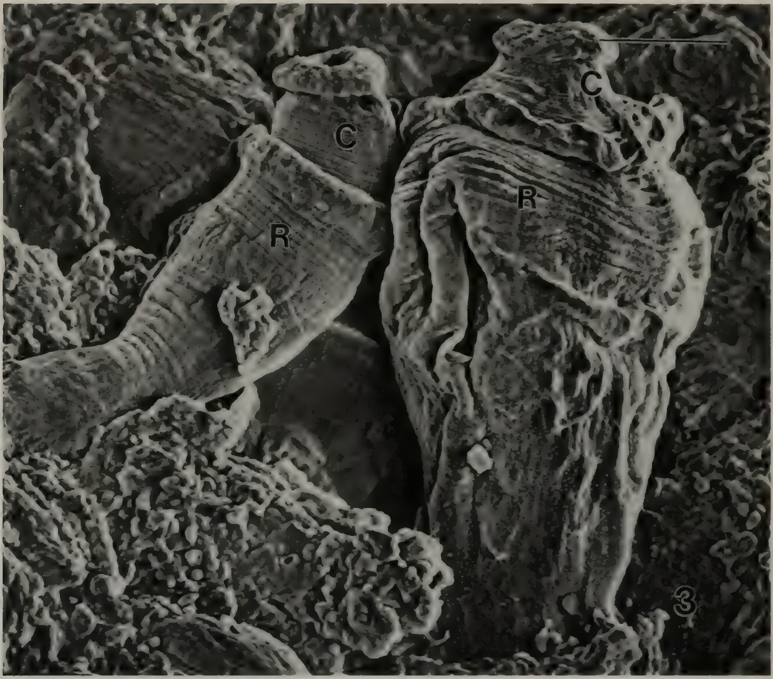


Fig. 1. Thin section, pleurolophocercous rediae from *Cerithidea*. Note two mature cercariae (arrows). Scale bar = 100μm. Fig. 2. SEM micrograph, pleurolophocercous rediae from *Cerithidea*. Note closed birthpore. Scale bar = 125μm. A = acetabulum, B = birthpore, C = cercariae, O = oral sucker, P = papillae, R = rediae, T = tail



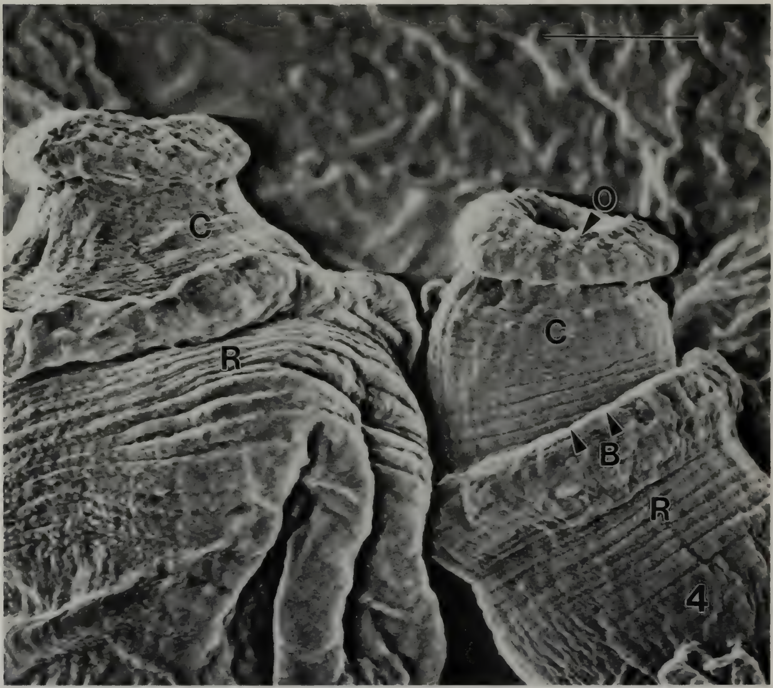
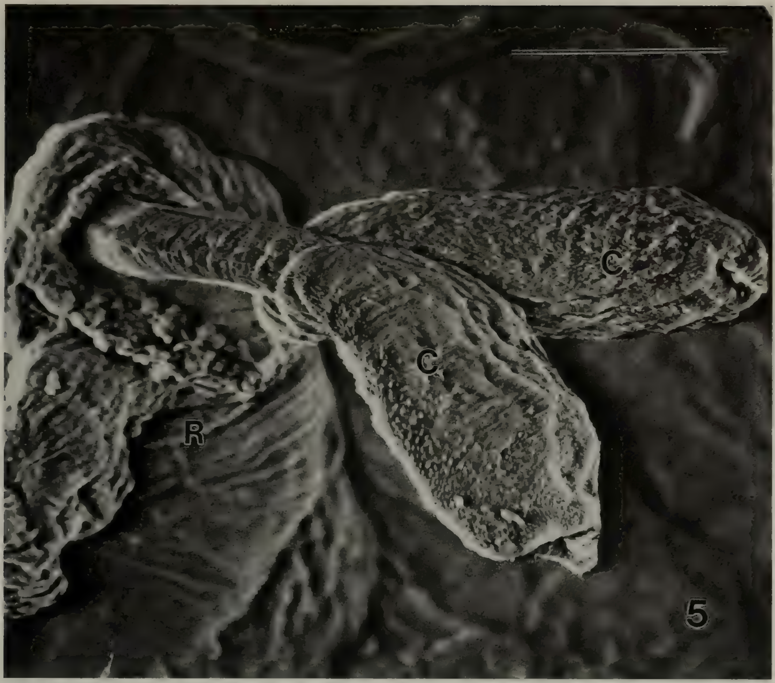


Fig. 3. SEM micrograph, pleurolophocercous rediae from *Cerithidea.* Only one cercaria is birthed at a time. Scale bar = 80μm. Fig. 4. SEM Micrograph, pleurolophocercous rediae from *Cerithidea.* Note annular ring around birthpore (arrows). Scale bar = 30μm.



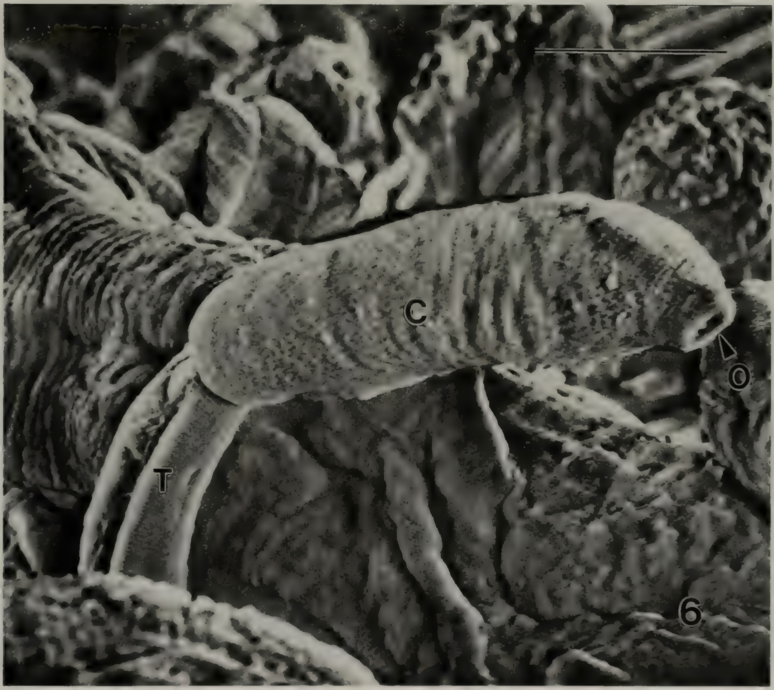
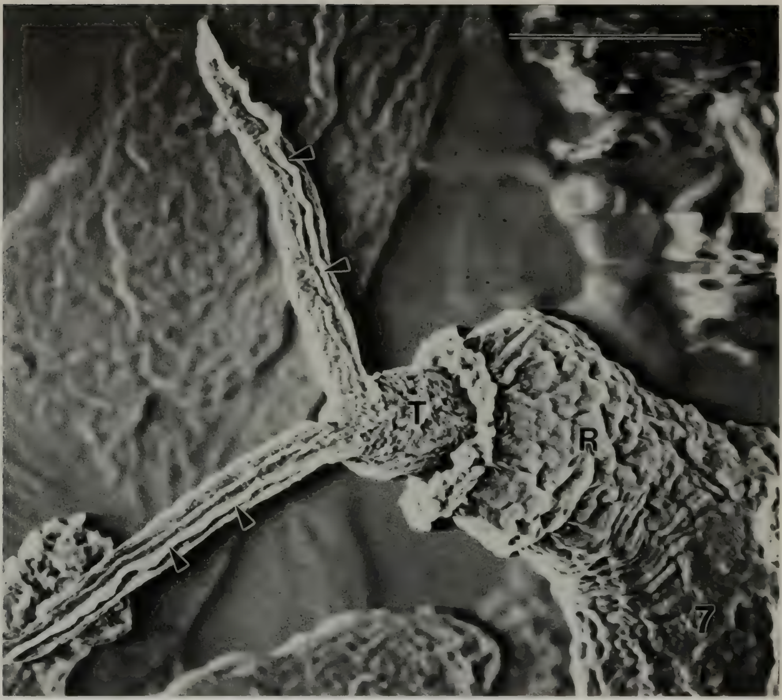


Fig. 5. SEM Micrograph, furcocercous rediae from *Cerithidea.* Multiple cercariae emerge simultaneously. Scale bar = 65μm. Fig. 6. SEM Micrograph, furcocercous rediae from *Cerithidea.* Note thick, muscular tail. Scale bar = 45μm.



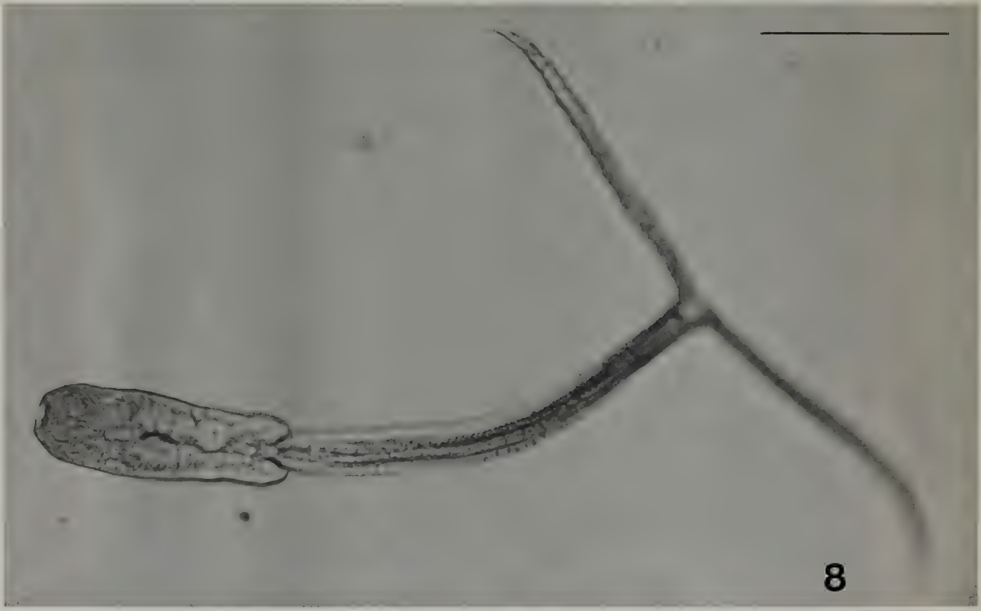
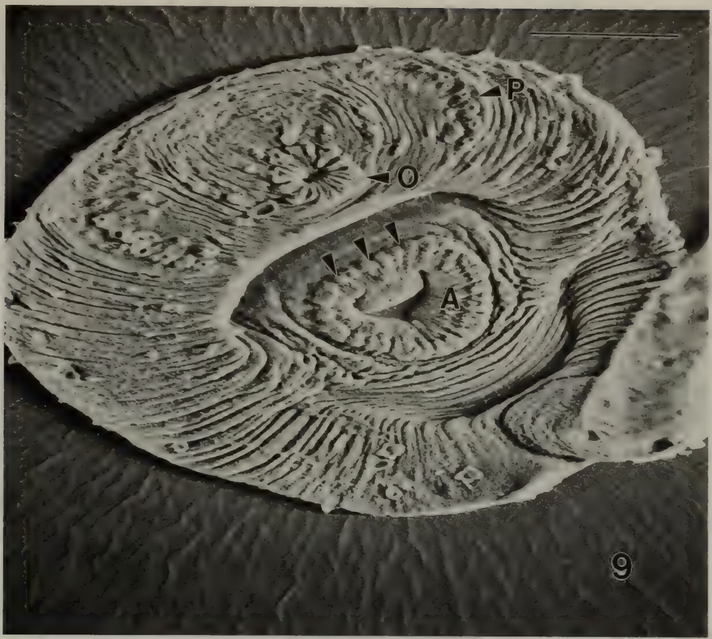
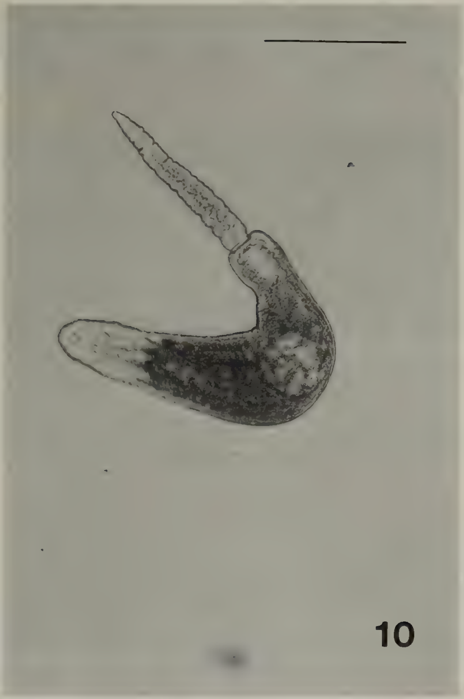


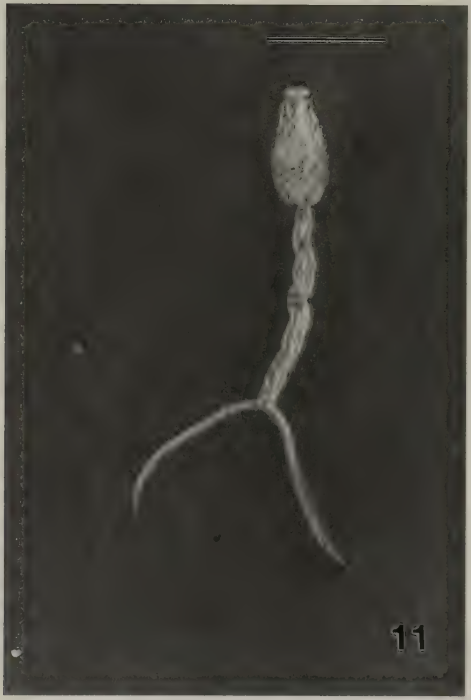
Fig. 7. SEM Micrograph, furcocercous rediae from *Cerithidea.* Often, these cercariae are birthed tail first. Note tail fins (arrows). Scale bar = 50μm. Fig. 8. Light Micrograph, furcocercous cercariae. Note length of tail relative to body. Scale bar = 80μm.



9



10



11

Fig. 9. SEM Micrograph, pleurolophocercous cercaria. Note massive acetabulum and papillae. Scale bar = 20μm. Fig. 10. Light Micrograph, pleurolophocercous cercariae, whole mount. Active worms stretch and compress in to a variety of shapes. Scale bar = 50μm. Fig. 11. Light Micrograph, furcocercous cercariae. Scale bar = 35μm.

(Phagicola) diminuta, and *Ascocotyle sexidigita* encysted in fish which also inhabit the same site (Armitage 1997, 1999). It cannot be discounted, however, that spines and bristles may have been lost in these specimens due to fixation artifact.

Literature Cited

Armitage, M. 1997 The euryhaline cottid fish, *Leptocottus armatus* (Girard), second intermediate host of the trematode *Ascocotyle (P.) diminuta.* Bull. So. Calif. Acad. Sci. 96(3):112–116.

——— 1999. The euryhaline gobiid fish, *Gillichthys mirabilis* Cooper 1864, second intermediate host of the trematode, *Pygidiopsoides spindalis* Martin 1951. Bull. So. Calif. Acad. Sci. 98(2):75–79.

Font, W. F., R. Heard and R. Overstreet. 1984. Life cycle of *Ascocotyle gemina,* n.sp., a sibling species of *A. sexidigita* (Digenea: Heterophyidae). Trans. Am. Micro. Soc. 103(4):392–407.

Martin, W. E. 1950a. *Euhaplorchis californiensis* N.G., N.Sp., Heterophyidae, Trematoda, with notes on its life-cycle. Trans. Am. Micro. Soc. 59(2):194–209.

——— 1950b. *Parastictodora hancocki,* N.G., N.Sp., (Trematoda: Heterophyidae), with observations on its life-cycle. J. Parasit. 36(4):360–370.

——— 1951. *Pygidiopsoides spindalis,* N.G., N.Sp., (Trematoda: Heterophyidae), and its second intermediate host. J. Parasit. 37(3):297–300.

——— 1955. Seasonal infections of the snail, *Cerithidea californica* Haldeman, with larval trematodes. Essays Nat. Sci. Honor of Capt. A. Hancock, 203–210. USC Press.

——— 1964. Life cycle of *Pygidiopsoides spindalis* Martin, 1951 (Heterophyidae: Trematoda). Trans. Am. Micro. Soc. 83:270–272.

——— 1972. An annotated key to the cercariae that develop in the snail *Cerithidea californica.* Bull. So. Calif. Acad. Sci. 71(1):39–43.

Maxon, M. G., and W. Pequegnat. 1949. Cercariae from upper Newport bay. J. Ent. Zool. 41:30–56.

Accepted for publication 19 June 2000.

INSTRUCTIONS FOR AUTHORS

The BULLETIN is published three times each year (April, August, and December) and includes articles in English in any field of science with **an emphasis on the southern California area**. Manuscripts submitted for publication should contain results of original research, embrace sound principles of scientific investigation, and present data in a clear and concise manner. The current AIBS *Style Manual for Biological Journals* is recommended as a guide for contributors. Consult also recent issues of the BULLETIN.

MANUSCRIPT PREPARATION

The author should submit *at least two additional copies with the original,* on 8½ × 11 opaque, nonerasable paper, double spacing the entire manuscript. *Do not break words at right-hand margin anywhere in the manuscript.* Footnotes should be avoided. **Manuscripts which do not conform to the style of the BULLETIN will be returned to the author.**

An abstract summarizing in concise terms the methods, findings, and implications discussed in the paper *must* accompany a *feature article. Abstract should not exceed 100 words.*

A feature article comprises approximately five to thirty typewritten pages. Papers should usually be divided into the following sections: abstract, introduction, methods, results, discussion and conclusions, acknowledgments, literature cited, tables, figure legend page, and figures. Avoid using more than two levels of subheadings.

A research note is usually one to six typewritten pages and rarely utilizes subheadings. Consult a recent issue of the BULLETIN for the format of *notes.* Abstracts are not used for notes.

Abbreviations: Use of abbreviations and symbols can be determined by inspection of a recent issue of the BULLETIN. **Omit periods after standard abbreviations:** 1.2 mm, 2 km, 30 cm, but Figs. 1–2. Use numerals *before* units of measurements: 5 ml, but nine spines (10 or numbers above, such as 13 spines). The metric system of weights and measurements should be used wherever possible.

Taxonomic procedures: Authors are advised to adhere to the taxonomic procedures as outlined in the International Code of Botanical Nomenclature (Lawjouw et al. 1956), the International Code of Nomenclature of Bacteria and Viruses (Buchanan et al. 1958), and the International Code of Zoological Nomenclature (Ride et al. 1985). Special attention should be given to the description of new taxa, designation of holotype, etc. Reference to new taxa in titles and abstracts should be avoided.

The literature cited: Entries for books and articles should take these forms.

McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus.* J. Mamm., 54:452–458.

Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

Tables should not repeat data in figures *(line drawings, graphs, or black and white photographs) or contained in the text.* The author must provide numbers and short legends for tables and figures and place reference to each of them in the text. Each table with legend must be on a separate sheet of paper. All figure legends should be placed together on a separate sheet. **Illustrations and lettering thereon should be of sufficient size and clarity to permit reduction to standard page size;** *ordinarily they* **should not exceed 8½ by 11 inches** in size and after final reduction lettering must equal or exceed the size of the typeset. All half-tone illustrations will have light screen (grey) backgrounds. Special handling such as dropout half-tones, special screens, etc., must be requested by and will be charged to authors. **As changes may be required after review, the authors should retain the original figures in their files until acceptance of the manuscript for publication.**

Assemble the manuscript as follows: cover page (with title, authors' names and addresses), abstract, introduction, methods, results, discussion, acknowledgements, literature cited, appendices, tables, figure legends, and figures.

A cover illustration pertaining to an article in the issue or one of general scientific interest will be printed on the cover of each issue. Such illustrations along with a brief caption should be sent to the Editor for review.

PROCEDURE

All manuscripts should be submitted to the Editor, Daniel A. Guthrie, W. M. Keck Science Center, 925 North Mills Avenue, Claremont, CA 91711. **Authors are requested to submit the names, addresses and specialities of three persons who are capable of reviewing the manuscript. Evaluation of a paper** submitted to the BULLETIN begins with a critical reading by the Editor; several referees also check the paper for scientific content, originality, and clarity of presentation. Judgments as to the acceptability of the paper and suggestions for enhancing it are sent to the author at which time he or she may be requested to rework portions of the paper considering these recommendations. The paper then is resubmitted and may be re-evaluated before final acceptance.

Proof: The galley proof and manuscript, as well as reprint order blanks, will be sent to the author. He or she should **promptly** and **carefully read** the proof sheets for errors and omissions in text, tables, illustrations, legends, and bibliographical references. He or she marks corrections on the galley (copy editing and proof procedures in *Style Manual*) and **promptly returns both galley and manuscript** to the Editor. Manuscripts and original illustrations will not be returned unless requested at this time. **All changes in galley proof attributable to the author (misspellings, inconsistent abbreviations, deviations from style, etc.) will be charged to the author. Reprint orders are placed with the printer, not the *Editor.***

CONTENTS

Pliocene Amphibians and Reptiles from Clark County, Nevada. Jim I. Mead and Christopher J. Bell 1

An Evolutionary Classification and Checklist of Amphibians and Reptiles on the Pacific Islands of Baja California, México. L. Lee Grismer 12

Spot Pattern of *Girella nigricans,* the California Opaleye: Variation among Cohorts and Climate Periods. Jana L. D. Davis 24

Diversity of Parasitic *Cuscuta* and their Host Plant Species in a *Larrea-Atriplex* Ecotone. Simon A. Lei 36

Persistence of the Nematode, *Oswaldocruzia pipiens* (Molineidae), in the Pacific Treefrog, *Hyla regilla* (Hylidae), from California. Stephen R. Goldberg and Charles R. Bursey 44

Cercarial Emergence from Rediae in California Snail Tissues. Mark Armitage 51

COVER: Light Micrograph, furcocercous cercariae from Cerithidea. Mark Armitage.

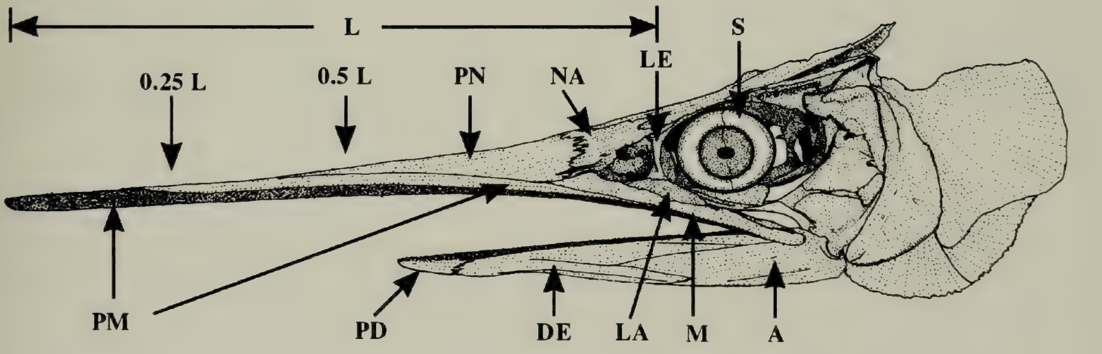
.S69
V.100:2

ISSN 0038-3872

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 100 **Number 2**


L
S
LE
0.25 L
0.5 L
PN
NA
PM
PD
DE
LA
M
A

CALIFORNIA
ACADEMY OF SCIENCES
OCT 17 2001
LIBRARY

BCAS-A100(2) 59–128 (2001) **AUGUST 2001**

Southern California Academy of Sciences

Founded 6 November 1891, incorporated 17 May 1907

OFFICERS

Daniel Pondella, *President*
Ralph Appy, *Vice-President*
Susan E. Yoder, *Secretary*
Daniel A. Guthrie, *Treasurer*
Daniel A. Guthrie, *Editor*
David Huckaby, *Past President*
Hans Bozler, *Past President*

BOARD OF DIRECTORS

1999–2002

Ralph G. Appy
Jonathan N. Baskin
John W. Roberts
Tetsuo Otsuki
Gloria J. Takahashi

2000–2003

James Allen
John Dorsey
Judith Lemus
Martha and Richard Schwartz
Susan E. Yoder

2001–2004

Brad R. Blood
Chuck Kopczak
Daniel Pondella
Raymond Wells
Raymond Wilson

Membership is open to scholars in the fields of natural and social sciences, and to any person interested in the advancement of science. Dues for membership, changes of address, and requests for missing numbers lost in shipment should be addressed to: Southern California Academy of Sciences, the Natural History Museum of Los Angeles County, Exposition Park, Los Angeles, California 90007-4000.

Professional Members	$35.00
Student Members	20.00

Memberships in other categories are available on request.

Fellows: Elected by the Board of Directors for meritorious services.

The Bulletin is published three times each year by the Academy. Manuscripts for publication should be sent to the appropriate editor as explained in "Instructions for Authors" on the inside back cover of each number. All other communications should be addressed to the Southern California Academy of Sciences in care of the Natural History Museum of Los Angeles County, Exposition Park, Los Angeles, California 90007-4000.

Date of this issue 11 September 2001

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

Bull. Southern California Acad. Sci.
100(2), 2001, pp. 59–73

A Fossil Blue Marlin (*Makaira nigricans* Lacépède) from the Middle Facies of the Trinidad Formation (Upper Miocene to Upper Pliocene), San José del Cabo Basin, Baja California Sur, México

Harry L. Fierstine,[1] Shelton P. Applegate,[2] Gerardo González-Barba,[3]
Tobias Schwennicke[3], and Luis Espinosa-Arrubarrena[2]

Biological Sciences Department, California Polytechnic State University,
San Luis Obispo, CA 93407, U.S.A.
[2]Instituto de Geologia, Universidad Nacional Autónoma de México,
Ciudad Universitaría, México, D.F., 04510, México
[3]Departamento de Geologia Marina, A.I. de Ciencias del Mar,
Universidad Autónoma de Baja California Sur, Apartado Postal #19B,
La Paz, Baja California Sur, 23080, México

Abstract.—A large fossil skull and several rostra of *Makaira nigricans* Lacépède, 1802 (Perciformes: Istiophoridae), as well as some less diagnostic istiophorid remains, have been recovered from the middle facies of the Trinidad Formation near Rancho Algodones, San José del Cabo Basin, Baja California Sur, México. These are the only billfish specimens known from fossiliferous deposits located between southern California and Panama. Based on published accounts of the presence of nannofossils and planktonic foraminifera, and additional field work, we conclude that the age of the study area is late Miocene to late Pliocene. Based on the habitat preferences of recent *M. nigricans* and on the type of sediments, we conclude that the middle facies of the Trinidad Formation was deposited far offshore at a water depth of at least 100 m in a bottom environment that was poorly oxygenated and without currents.

The blue marlin, *Makaira nigricans* Lacépède, 1802, is an important commercial and recreational fish species that inhabits the tropical and temperate Atlantic, Indian, and Pacific oceans favoring depths of over 100 m and temperatures of approximately 24°C (Nakamura 1983, 1985). Blue marlin are usually distributed from about 45°N latitude to 35°S latitude in the Pacific Ocean (Nakamura 1983), although in the far Eastern Pacific blue marlin generally range only from 23°N to 3°S (Rivas 1975). *Makaira nigricans* is occasionally observed off southern California, but only during periods of anomalously high sea surface temperatures (National Marine Fisheries Service [The Southwest Fisheries Science Center's 1996 Billfish Newsletter], unpublished).

Fossil remains of blue marlin or blue marlin-like fish (e.g., *Makaira* sp., cf. *M. nigricans*) are reported from the middle Miocene of Belgium, from the late Miocene of Panama, southern California and Virginia, and from the early Pliocene of North Carolina (Fierstine 1998, 1999, 2001). Discovery of a large skull and several rostra of *M. nigricans,* as well as some less diagnostic istiophorid remains, in the middle facies of the Trinidad Formation (late Miocene to late Pliocene) in the San José del Cabo Basin, Baja California Sur, México, offers the first opportunity to examine billfish specimens from fossil deposits located between southern

California and Panama and to discuss the paleoecology of the Trinidad Formation based on the habitat preference of a still extant bony fish. Interpretations of the stratigraphy, ages and depositional environments of the rocks near Rancho Los Algodones are equivocal (Espinosa-Arrubarrena 1979; McCloy 1984; Martínez-Gutiérrez and Sethi 1997) and we offer our own conclusions based on additional field work and information from recent publications.

Materials and Methods

The materials and methods used in this study, particularly for the rostrum, have been described fully in Fierstine and Voigt (1996) and Fierstine (1998, 1999, 2001), but some of it is repeated here for convenience. Approximately 160 whole and partial skeletons of Recent specimens representing seven species of the family Istiophoridae were examined and used for comparisons with the fossil material. The museum number, geological age, and locality are given in the text for each fossil specimen that was used as comparative material.

Anatomical abbreviations: A, articular; DE, dentary; LA, lacrimal; LE, lateral ethmoid; M, maxillary; NA, nasal; NC, nutrient canal; PD, predentary; PM, premaxilla; PN, prenasal; S, sclerotic; † denotes extinct taxon.

Institutional abbreviations: IGM, Instituto de Geología, Ciudad Universítaría, Universidad Nacional Autónoma de México, D.F., México; LACM, Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.

Characters and their definitions for each bone or structure are as follows:

Rostrum.—Fierstine (1998, 1999) and Fierstine and Voigt (1996) emphasized two regions of the rostrum in Recent specimens (Fig. 1): 0.5L, or one-half the distance between the distal tip and the orbital margin of the lateral ethmoid bone (L); and 0.25L, or one-fourth the distance between the distal tip and the orbital margin of the lateral ethmoid bone. Six morphometric characters were studied in each region (Fig. 1): depth (D) and width (W) of rostrum; height (H) and width (N) of the left nutrient canal (as seen in cross-section); distance (IC) between the right and left nutrient canals (as seen in cross-section); and distance (DD) of the left nutrient canal from the dorsal surface of the rostrum (as seen in cross-section). Characters studied without reference to region were: distribution of denticles on the dorsal surface of the rostrum measured from the distal tip (DZ); length from distal tip where denticles are absent from the ventral mid-line (DVS); length from the distal tip to the distal extremity of the prenasal (P); length from tip where fused premaxillae divide into separate bones (VSPM); and presence or absence of denticles on the prenasal.

In the fossil specimens from San José del Cabo (Figs. 2–3; Table 1); the exact position of 0.5L or 0.25L was unknown and cross-sections were studied at broken end(s) or from computer tomography images. No transverse cuts were made of the specimens. Using the techniques of Fierstine and Crimmen (1996) and Fierstine (2001), a cross-section was estimated to be at 0.5L if the prenasal bone was large, and at 0.25L if the prenasal bone was tiny or absent. Because of the fragmentary nature of the fossil rostra, DZ was the only character available to study in each estimated region.

Predentary.—Fierstine (1998, 2001) studied three morphometric characters in Recent and fossil specimens: length along the ventral mid-line (PL), width across the widest expanse of the denticulated surface (PW), and depth perpendicular to

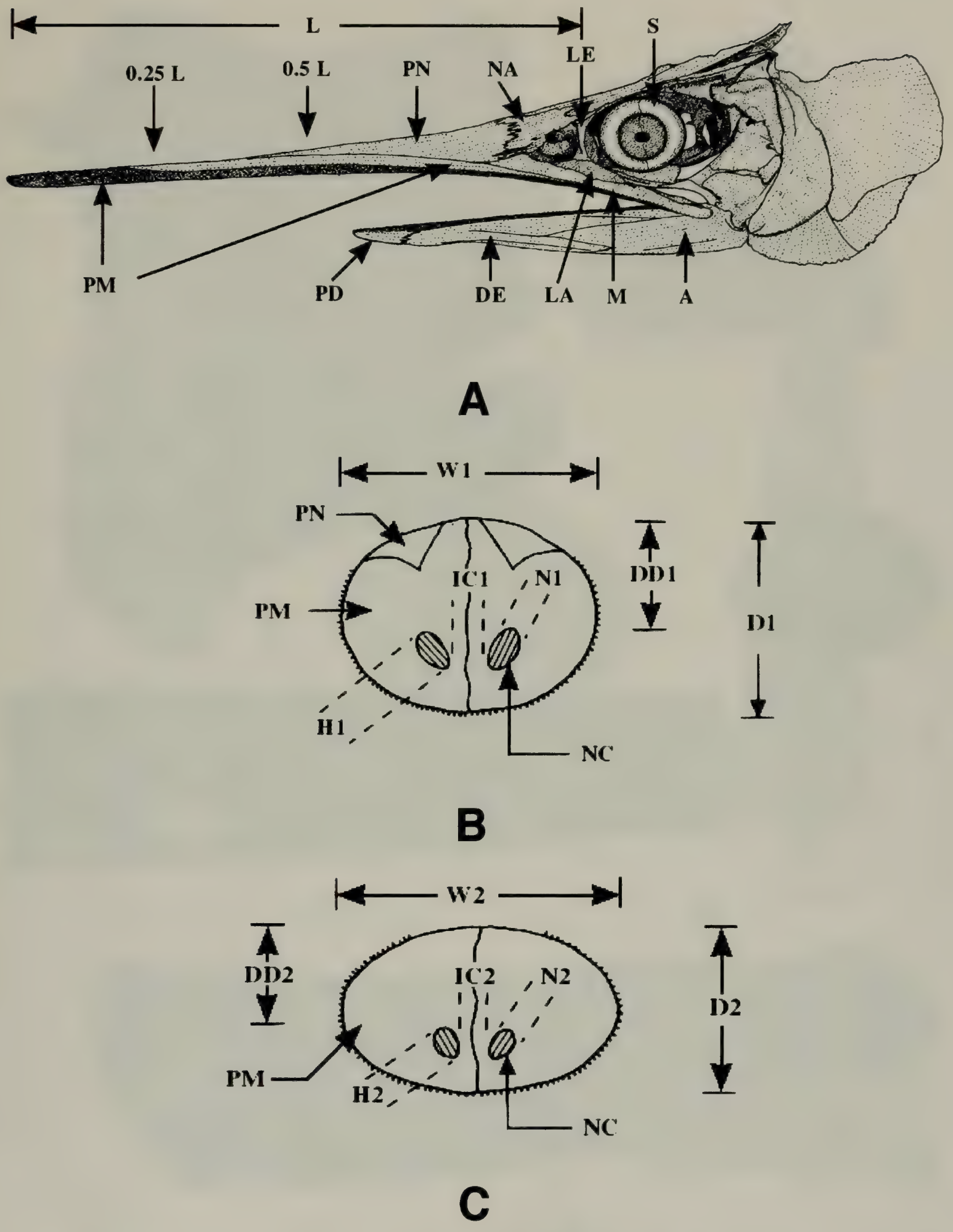

L
S
LE
0.25 L
0.5 L
PN
NA
PM
PD
DE
LA
M
A
A
W1
PN
IC1
N1
DD1
PM
D1
H1
NC
B
W2
DD2
IC2
N2
D2
PM
H2
NC
C

Fig. 1. *Makaira nigricans* Lacépède. A. Skull, left lateral view. Drawing is a composite of two Recent specimens (LACM 25491 and 46023-1). B. Enlarged cross-section of generalized istiophorid rostrum at one-half bill length (0.5L). C. Enlarged cross-section of generalized istiophorid rostrum at (0.25L). See text for definition of abbreviations (modified from Fierstine, 1999:fig. 3 and Fierstine and Voigt, 1996:fig. 2).

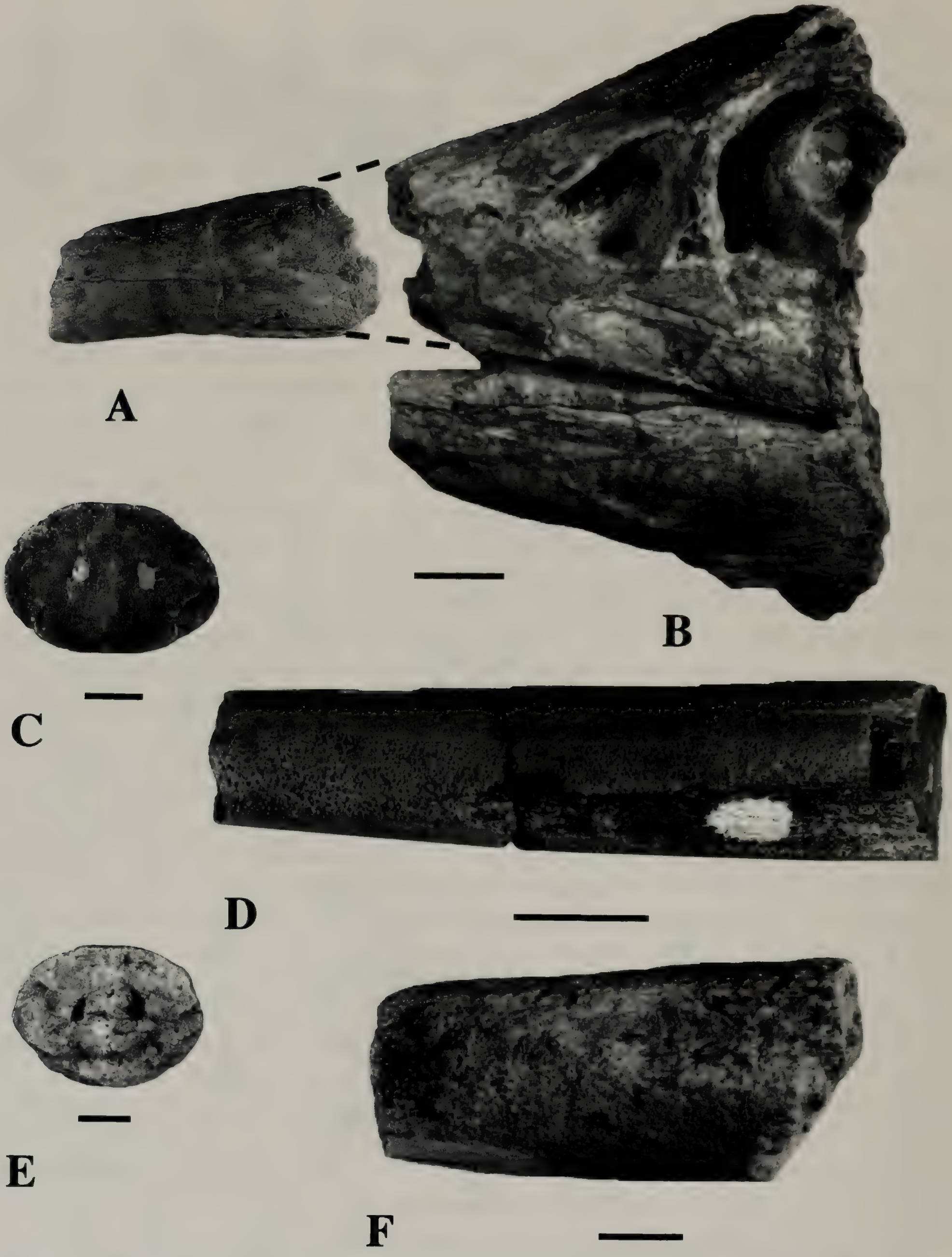


Fig. 2. *Makaira nigricans* Lacépède, upper Miocene-late Pliocene, middle facies of the Trinidad Formation, San José del Cabo Basin, Baja California Sur, México. A. Proximal rostrum (IGM 7888), left lateral view. B. Partial skull (IGM 7889), left lateral view. Dotted lines indicate probable attachment of A with B. C. Partial rostrum (IGM 7884), posterior view. D. Lateral view of C. E. Partial rostrum (IGM 7893), anterior view. F. Lateral view of E (IGM 7893). Scale bar equals 5 cm (A, B), 2 cm (D), and 1 cm (C, E, and F).

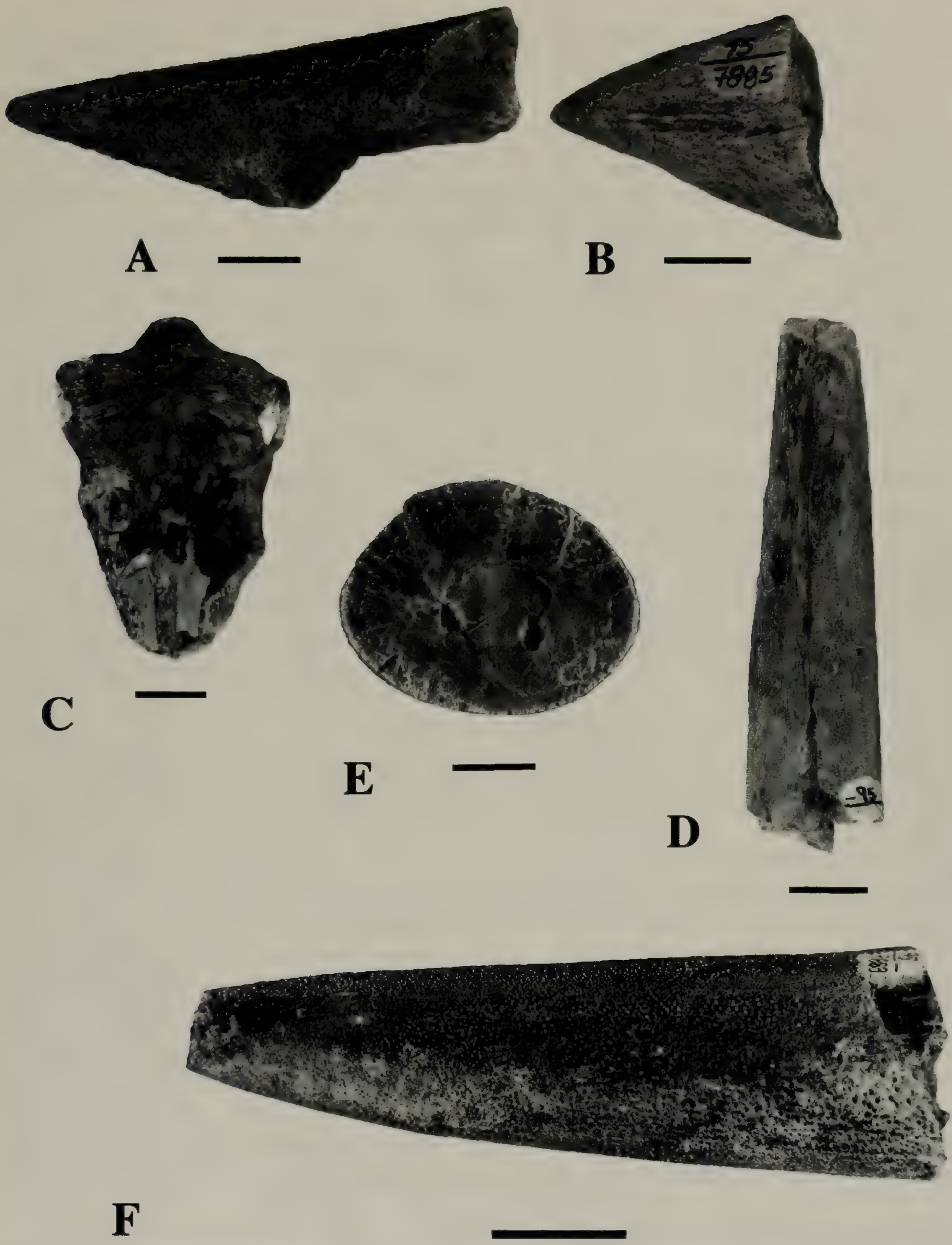


Fig. 3. Istiophorid billfish fossils, upper Miocene-late Pliocene, middle facies of the Trinidad Formation, San José del Cabo Basin, Baja California Sur, México. A. Istiophoridae gen. and sp. indet., partial predentary, dorsal view (IGM 7887). B. Istiophoridae gen. and sp. indet., partial predentary, dorsal view (IGM 7885). C. Istiophoridae gen. and sp. indet., partial ?dorsal pterygiophore (IGM 7894), anterior view. E. *Makaira* sp., cf. *M. nigricans* Lacépède, partial rostrum, posterior view (IGM 7883). F Lateral view of E (IGM 7883). Scale bar equals 1 cm (A–E) or 2 cm (F).

Table 1. Measurements and ratios of partial rostra of five specimens of the Family Istiophoridae from the San Jose del Cabo Basin, Trinidad Formation (upper Miocene to late Pliocene), Baja California Sur, México. Measurements taken from computer tomography images are indicated with a pound sign (#) and measurement and ratio estimates are indicated with an asterisk (*). Region refers to whether the bill was studied as part of 0.25L or 0.5L (see text for definitions).

			Measurements (in mm)							Ratios				
Specimen number	Locality number	Region	Overall length	W	D	H	DD	IC	DZ	D/W	H/D	DD/D	IC/W	DZ/W
IGM 7882	IG 95	0.25L	159.0	29.7#	18.6#	03.2#	09.3#	05.3#	13.0	0.63	0.17	0.50	0.18	0.44
IGM 7883	IG 95	0.25L	108.4	42.0	33.6	05.0	19.7	08.0	99.5*	0.82	0.15	0.59	0.19	2.37*
IGM 7884	IG 95	0.25L	116.9	41.6	28.7	05.3	11.8	08.9	—	0.69	0.18	0.41	0.21	—
IGM 7888	IG 95	0.5L	220.0	101.6#	80.3#	07.5#	41.8#	17.8#	—	0.79	0.09	0.52	0.18	—
IGM 7893	IG 93	0.25L	60.5	37.0	28.8	04.2	09.5	07.7	—	0.78	0.15	0.33	0.21	—

the long axis from PW to the ventral surface of the bone (PD). The San José del Cabo specimens (Fig. 3) were too fragmentary to obtain any of the three morphometric characters.

Skull.—Although there are published descriptions available of a typical or specific istiophorid skull (Gregory and Conrad 1937; Schultz 1987; Davie 1990), there are no comparative osteological studies that are useful in determining the species represented by the partial skull from the San José del Cabo Basin (Fig. 2B). Nakamura (1983, 1985) compared complete neurocrania of Recent istiophorid species and found generic differences in overall proportions. Fierstine (1998, 2001) found specific differences among three isolated skull bones (articular, maxilla, and parasphenoid) of Recent and fossil istiophorids, but those features are not preserved in the fossils from the San José del Cabo Basin. Identification of the skull is based on overall size and its possible attachment to one of the rostra (IGM 7888).

Pterygiophore.—Potthoff et al. (1986:672, fig. 14) described the development of pterygiophores in the anal and dorsal fins of istiophorids, but we are not aware of any published morphological accounts of individual pterygiophores in the adult Istiophoridae. Identification of the partial pterygiophore (IGM 7894) from San José del Cabo Basin (Fig. 3) is based on comparison with pterygiophores in the dorsal and anal fins of three Recent istiophorids, LACM 46023-1 (*M. nigricans*), LACM 25509 (*M. indica*), and LACM 25499 (*T. angustirostris*).

Regional Geology

The Buena Vista-San José del Cabo Basin is located near the southern end of the Baja California Peninsula between the Sierra La Laguna and Sierra La Trinidad mountain ranges (Fig. 4). Both ranges are composed of crystalline and metamorphic rocks. Based on evidence from fission-track thermochronology, Fletcher et al. (2000) suggested that the uplift of the Sierra La Laguna Mountains along the San José del Cabo fault started approximately 10–12 Ma. The basin covers approximately 2,000 km^2 and contains both terrestrial and marine strata that range in age from early middle Miocene to Recent (McCloy 1984; Martínez-Gutiérrez and Sethi 1997). Martínez-Gutiérrez and Sethi (1997) considered the basin to have formed in association with the opening of the Gulf of California and formation of the Baja California Peninsula, and proposed a general model for its evolution. The sedimentary rocks of the basin filling are mainly dipping to the southwest or west, and for this reason the oldest sedimentary rocks are exposed along the eastern margin of the basin, becoming younger to the southwest and west. The presence of faults complicates this general picture.

The Calera Formation (Fig. 5) is the oldest sedimentary and non-marine unit in the basin (Martínez-Gutiérrez and Sethi 1997), and is composed of sandstones and conglomerates deposited in an alluvial fan environment. Its age is uncertain due to the lack of fossils, but McCloy (1984) assigned an age of no younger than middle Miocene, and Martínez-Gutiérrez and Sethi (1997) considered the beds to be middle Miocene to late Miocene, an age range that essentially agrees with the fission-track data of Fletcher et al. (2000), if the basin began to fill with deposits soon after uplift of the Sierra La Laguna Mountains. The superposed Trinidad Formation (Fig. 5) was deposited in a nearshore to basinal marine setting during the middle Miocene to upper Pliocene (see discussion below). The marine Refugio

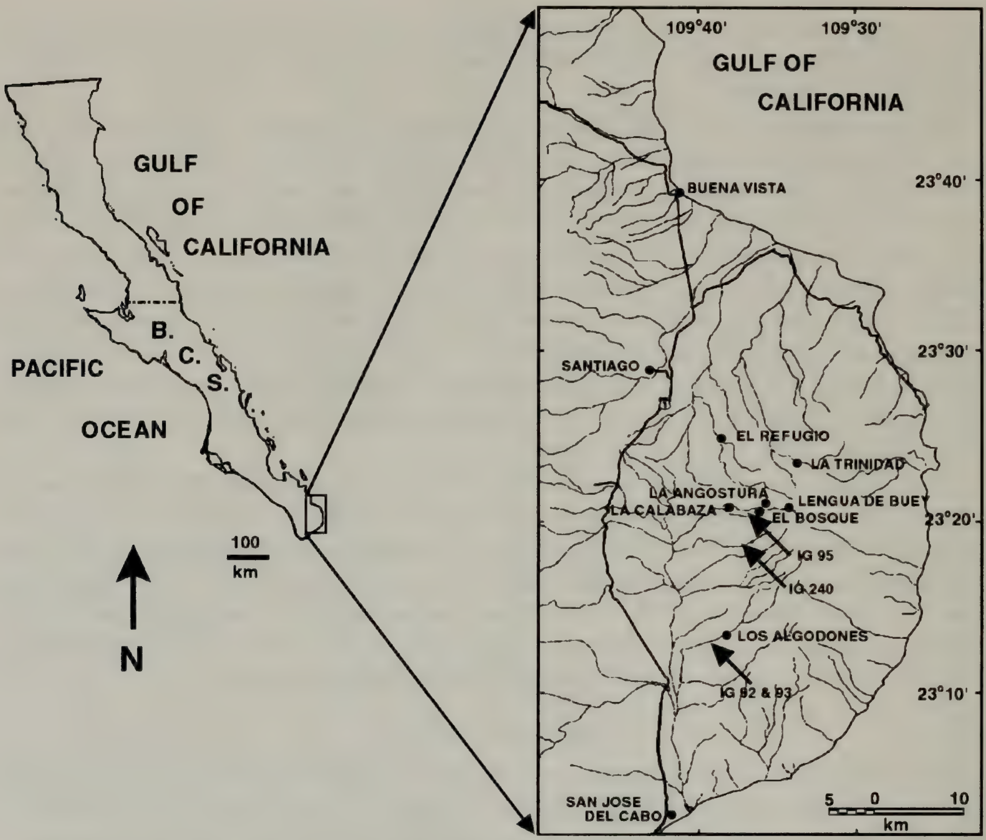

GULF
OF
CALIFORNIA
B.
C.
S.
PACIFIC
OCEAN
100
km
N
109°40'
109°30'
GULF OF
CALIFORNIA
BUENA VISTA
23°40'
23°30'
SANTIAGO
EL REFUGIO
LA TRINIDAD
LA ANGOSTURA
LA CALABAZA
LENGUA DE BUEY
EL BOSQUE
23°20'
IG 95
IG 240
LOS ALGODONES
IG 92 & 93
23°10'
SAN JOSE
DEL CABO
5 0 10
km

Fig. 4. Map of southern Baja California Sur, México (B.C.S.), indicating collection localities for istiophorid billfish in the middle facies of the Trinidad Formation (upper Miocene-late Pliocene), San José del Cabo Basin. (modified from Martínez-Gutiérrez and Sethi, 1997:figs. 1,2).

Formation (Fig. 5) overlies the Trinidad Formation and the contact between them is transitional as well as erosional (Martínez-Gutiérrez and Sethi 1997). The Refugio Formation is composed of siltstones, sandstones, and limestones. Many sandstones are cross-bedded and fossiliferous, indicating nearshore depositional settings. McCloy (1984) suggested a late Pliocene age for the Refugio Formation, whereas Smith (1991) and Martínez-Gutiérrez and Sethi (1997) considered it to be early Pliocene.

The Trinidad Formation

The Trinidad Formation is the oldest marine stratigraphic unit in the Buena Vista-San José del Cabo basin. McCloy (1984) estimated its thickness to be between 700 and 1000 m, whereas Martínez-Gutiérrez and Sethi (1997) estimated its thickness at 400 m. McCloy (1984) informally divided the formation into four lithologic subunits (A to D). Subunit A is generally a sequence that grades upward from course to fine and is composed of cross-bedded or planar-bedded sandstone, siltstones, and fissile and laminated shales. These beds may have alternating tan to buff siltstones and gray shales with sandstone intercalations. Fossils (mainly mollusks) are common and McCloy (1984) interpreted the unit as inner to outer shelf deposits. Subunit A is well-exposed around Rancho Lengua de Buey (N 23° 20.318′, W 109° 33.910′). Subunit B, a succession of sandstone, siltstone, and alternating beds of sandstone and mudstone, is related to an outermost shelf to upper shelf depositional environment. Sedimentary structures (graded beds, cross-bedding) indicate traction and downslope transport of sandy sediments (McCloy 1984). We found outcrops of this unit at Rancho El Bosque (N 23° 20.53′, W 109° 36.378′). Subunit C is a succession of mudstones, diatomaceous shales, and diatomite that displays a transitional or marked rhythmic cyclicity often with fine laminae. McCloy (1984) and Carreño (1992) found massive diatomites in the central part of the basin, and McCloy (1984) proposed that they were deposited in a partially aerated to anoxic environment. We found good outcrops of subunit C in Cañada del Enmedio. Subunit D consists of greenish, laminated, non-bioturbated, clayey siltstones that grade upward into massive to cross-bedded bioturbated, fossiliferous sandstones. McCloy (1984) suggested these sediments were deposited in an outer shelf environment. Subunit D is well-exposed near Rancho La Calabaza (N 23° 20.71′, W 109° 38.252′).

Martínez-Gutiérrez and Sethi (1997) subdivided the Trinidad Formation into three vertically stacked lithofacies. The basal facies is approximately equivalent to McCloy's (1984) subunit A and was interpreted as representing nearshore to lagoonal, brackish-marine deposits. The middle facies is equivalent to McCloy's subunits B and C, and was interpreted as having been deposited in "shelf depths slightly greater than that of normal wave base" (Martínez-Gutiérrez and Sethi 1997). We believe the middle facies was deposited in much deeper water that was influenced initially by turbidity currents (subunit B). The presence of non-bioturbated diatomaceous sediments in subunit C indicates a low sedimentation rate in a basinal setting. The upper facies corresponds to McCloy's (1984) subunit D, and Martínez-Gutiérrez and Sethi (1997) suggested that it was deposited in a high energy, shallow marine depositional environment, an interpretation that is consistent with our observations.

The Trinidad Formation has been assigned different ages. McCloy (1984) considered it to span middle? Miocene to late Pliocene. She gave a late Pliocene age for subunit C based on microfossils. Carreño (1992) demonstrated an uppermost ?Miocene/early Pliocene to middle Pliocene age for beds exposed near the town of Santiago that approximately correspond to McCloy's subunits B and C. However, according to Berggren et al. (1995), the microfossils reported by Carreño extend into the late Pliocene. In contrast, Martínez-Gutiérrez and Sethi (1997) suggested an age from late Miocene to early Pliocene, but did not present new evidence for their conclusion. In conclusion, the total stratigraphic range for the Trinidad Formation probably spans from middle Miocene to upper Pliocene.

The billfish fossils described herein were recovered from several localities. Locality IGM 95 (N 23° 20.400′, W 109° 36.931′): is located in a westward dipping sequence, known informally as La Angostura, that is exposed west of Rancho El Bosque (Fig. 4). It consists of 40 m of diatomaceous mudstone and clayey siltstone that probably correspond to McCloy's (1984) subunit C. In the upper part of the outcrop there are abundant large, yellow-weathering limestone concretions that contain the billfish fossils that we report here.

Locality IGM 240 (N 23° 20.550′, W 109° 39.537′) is located in a westward dipping sequence that is exposed in Cañada del Enmedio (Fig. 4). A 55 m thick stratigraphic section contains diatomaceous mudstone at its base and is transitional upward to clayey siltstone and then to siltstone at the top. These beds mark the transition between McCloy's (1984) subunits C and D. The upper part of this stratigraphic section has yellow-weathering concretions some of which contain remains of fossil billfish similar to those collected at locality IG 95.

Other fossil localities are located in the area around Rancho Algodones (N 23° 13.200′, W 109° 38.450′) (Fig. 4). Locality IGM 92 (Los Algodones) includes exposures distributed southwest of the ranch. Locality IGM 93 (Los Dientes Grandes) is situated about 1 km southwest of the ranch, and corresponds to locality BCS-7 of Espinosa-Arrubarrena (1979). Barnes (1998) reported that locality IGM 92 has yielded the remains of mysticete and odontocete whales, and locality IGM 93 has yielded mysticete whales and a possible odobenine walrus. The rocks exposed in this region have been reported as Refugio Formation (formerly called Salada Formation) by Espinosa-Arrubarrena (1979), Espinosa-Arrubarrena and Applegate (1981), and Barnes (1998), but for reasons given below, we now believe they are part of the Trinidad Formation. The geologic map of Martínez-Gutiérrez and Sethi (1997:figs. 2, 11) only shows the Refugio Formation in this region although a stratigraphic section made near the ranch includes the Trinidad Formation in its lower part. In our field work we noted that the strata in this area generally dip 10–20°W. There are no major faults. The ranch rests on beds of the lower or lower middle Trinidad Formation and lithologic features exposed near the ranch fit subunit B of McCloy (1984). Topographically higher areas are partly covered by Pleistocene terrace deposits that earlier workers might have confused with the Refugio Formation. East of the Rancho Algodones the Trinidad Formation disconformably overlies granitic basement rocks. The gradational contact with the superposed Refugio Formation is well exposed 2 km to the west and southwest of the ranch and, because of the striking lithologic differences between the two formations, the Refugio and Trinidad Formations are easily separated in the field. The general lithology of the Trinidad Formation, dominated by greenish shale and siltstone, agrees with differences noted in the more northerly areas. However, we did not observe the diatomites that are typically found in the middle part of the formation.

Espinosa-Arrubarrena (1979) and Espinosa-Arrubarrena and Applegate (1981) suggested a late Pliocene age for the selachian fauna of locality IGM 92 (Los Algodones) based on the stratigraphic ranges of the shark species, and a similarity between the invertebrate fauna that was collected at Espinosa-Arrubarrena's locality BCS-43 and faunas in the Imperial Formation in California and the San Marcos Formation near Santa Rosalía, Baja California. However, the Imperial Formation is now thought to range from the late Miocene to late Pliocene in age (McDougall et al. 1999) and the San Marcos Formation is now known to be late Miocene based on radiometric data (Smith, 1991). The selachian fauna by itself offers little help in determining the exact age of the Trinidad Formation in the Los Algodones area because it includes species that range from the late Miocene and Pliocene to Recent (Espinosa-Arrubarrena 1979; Espinosa-Arrubarrena and Applegate 1981:table 1).

In conclusion, the fossils described below came from the middle to upper part of the Trinidad Formation, probably corresponding to McCloy's (1984) subunits B and C. We can not give a precise age, but believe the age for these subunits in our study area to be late Miocene to late Pliocene. The specimens probably settled to the bottom in a poorly oxygenated environment that lacked bottom currents.

Systematic Paleontology
Class Actinopterygii (sensu Nelson, 1994)
Division Teleostei (sensu Nelson, 1994)
Order Perciformes (sensu Johnson and Patterson, 1993)
Suborder Scombroidei (sensu Carpenter et al., 1995)
Family Istiophoridae (sensu Robins and deSylva, 1960)
Istiophoridae, genus and species indet.
Figs. 3A–D

Specimens.—Locality IGM 92: numerous fragments of a large rostrum, uncatalogued; partial pterygiophore (?dorsal fin), IGM 7894. Locality IGM 95: three predentaries, IGM 7885–7887; two median fin spine fragments, IGM 7890–7891; pectoral fin spine fragment, IGM 7892. IGM 240: distal rostral fragments, uncatalogued.

Discussion.—These bones are too fragmentary to be positively identified to genus, however, the rostra, pterygiophore, fin spines, and two predentaries are from fish of large size, a factor that favors their identification as belonging to the genus *Makaira* or *Tetrapturus audax,* and not to the genus *Istiophorus* nor to *T. albidus, T. angustirostris, T. belone,* or *T. pfluegeri.* The pterygiophore is a distal fragment. Its shield-like shape, the stellate pattern on its anterior and posterior surfaces for articulation with the pterygiophore anterior and posterior to it, and the broad articular surface for the fin spine, are characteristic features of a pterygiophore from the anterior part of the dorsal or anal fin in the Istiophoridae. It is similar in morphology to the pterygiophore that supports the 3rd or 4th dorsal spine, but because of a lack of comparative skeletal material, we can not eliminate the possibility it supported an anal spine. The uncatalogued specimens from localities IGM 92 and IGM 240 were examined by one of us (HLF) in 1984, but subsequently were discarded, lost, or misplaced before they could be accessioned by IGM.

Genus *Makaira* Lacépède, 1802
Makaira sp., cf. *M. nigricans* Lacépède, 1802
Figures 3E, F

Specimens.—Locality IGM 95: distal rostrum, IGM 7883.

Discussion.—Although two ratios (D/W and DD/D) fall only within the observed range of values computed for *M. nigricans* and not within the range of any other Recent istiophorid (Table 1), the rostrum was not positively identified as belonging to *M. nigricans.* The dorsal surface of the rostrum was completely covered with denticles, yielding a very large DZ/W value, a feature unknown in any Recent or fossil *M. nigricans* (Fierstine 1999: Tables 2, 3).

Makaira nigricans Lacépède, 1802
Figures 2A–F

Specimens.—Locality IGM 93: distal rostrum, IGM 7893. Locality IG 95: two distal rostra, IGM 7882, 7884; proximal rostrum, IGM 7888; partial skull, IGM 7889.

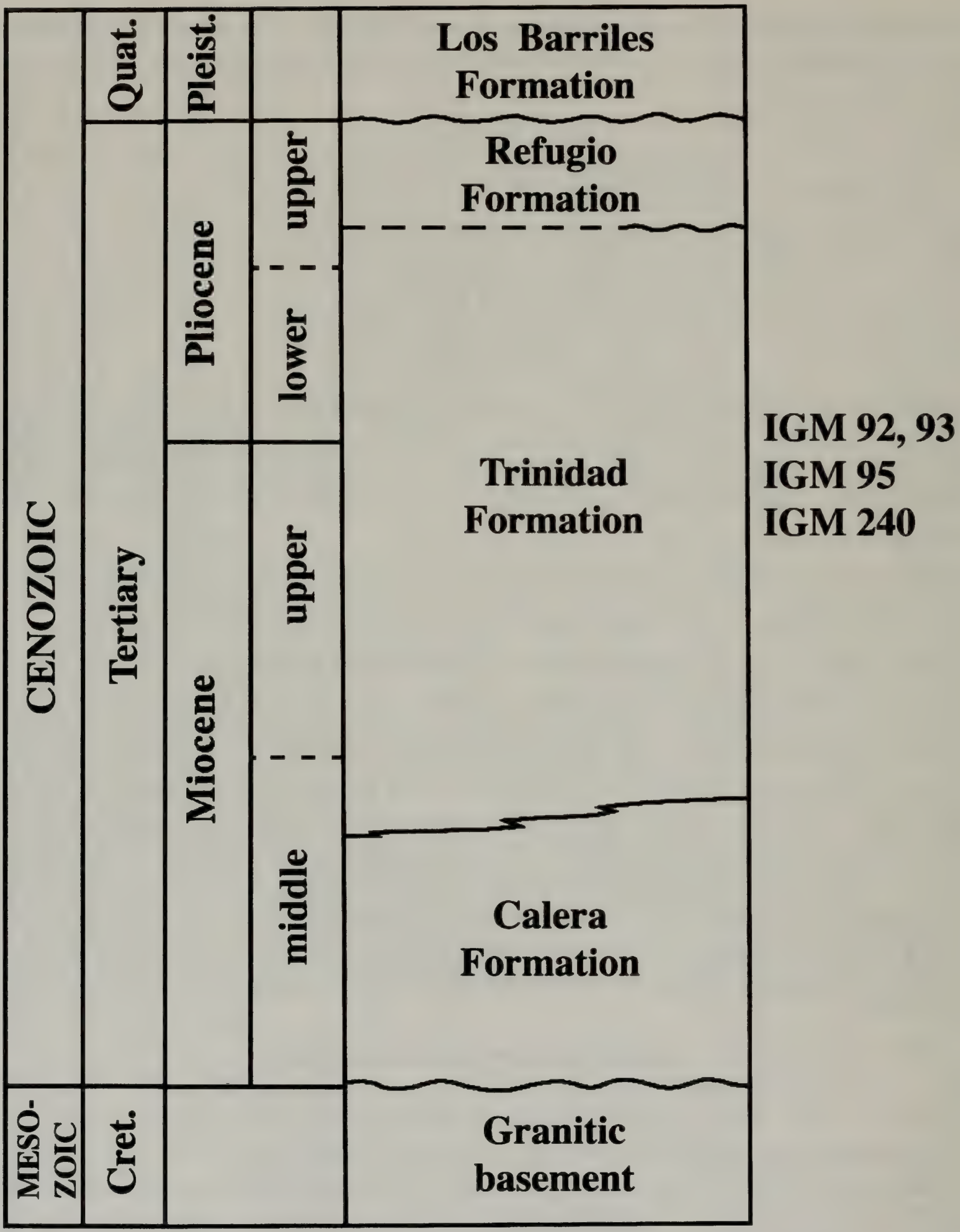

MESO-ZOIC
CENOZOIC
Cret.
Tertiary
Quat.
Pleist.
Pliocene
Miocene
upper
lower
upper
middle
Los Barriles Formation
Refugio Formation
Trinidad Formation
Calera Formation
Granitic basement
IGM 92, 93
IGM 95
IGM 240

Fig. 5. Stratigraphic column of beds near Rancho Algodones, San José del Cabo Basin, Baja California Sur, México.

Discussion.—All ratios (Table 1) computed for the above rostra are within the range of values observed for Recent *M. nigricans* with one exception, ratio IC/W for IGM 7888. Specimen IGM 7888 was identified as belonging to *M. nigricans* for two reasons: 1) ratio IC/W is not within the observed range of values of any fossil or Recent istiophorid, but is closest to the value of Recent *M. nigricans* (Fierstine 1999: Tables 2, 3), and 2) ratio DD/D is only within the observed range of Recent *M. nigricans.* The partial skull (IGM 7889) has no osteological feature that is diagnostic of *M. nigricans,* however, its identification is based on our belief that both rostrum IGM 7888 and the skull are from the same individual. The skull and rostrum belong to a similar-sized fish and both were encased in a sandy matrix that contained small veins of calcite.

The partial skull is a fully articulated unit from mid-orbit to the base of the rostrum and it has an overall length of 308 mm and a posterior width of 245 mm. The left side is more complete than the right side. The neurocranium contains the anterior-most part of the frontals, lateral ethmoids, nasals, and posterior parts of the prenasals. The olfactory foramen of the lateral ethmoid is visible in the nasal fossa. The thin portion of the frontals that covers the pineal apparatus (Rivas 1953) on the mid-dorsal surface of the skull is not preserved and the pineal fossa is exposed. The left orbit contains the anterior half of the sclerotic.

The maxillary segment contains its anterior articulation with the prenasal, dorsal articulation with the lacrimal, and ventral articulation with the premaxilla. The lower jaw contains the entire articular-dentary suture. Denticles are visible on both the dentary and premaxilla.

Both the dorsal-ventral diameter (115 mm) of the sclerotic (IGM 7889) and the width of the skull (IGM 7889) across the lateral ethmoids (248 mm) are approximately 1.4 times greater than similar measurements of a 181 kg Recent *M. nigricans* (LACM 46023-1). Assuming that IGM 7889 came from a specimen with a length (tip of bill to fork of caudal fin) that was 1.4 times longer than LACM 46023-1 (3280 mm), then the skull (IGM 7889) and rostrum (IGM 7888) probably are remains of a fish larger than 500 kg, based on the length-weight curve published in Strasburg (1969). Individuals of Recent *M. nigricans* that are larger than 160 kg are always females (Hopper 1986:60).

Discussion and Conclusions

The presence of *M. nigricans* in a marine upper Miocene or Pliocene deposit in Baja California Sur is not surprising because it has been the most common billfish identified in Neogene deposits bordering the eastern North Pacific Ocean from southern California to Panama (Fierstine and Applegate 1968; Fierstine and Welton 1988; Fierstine, 1999), and it is commonly caught off Cabo San Lucas, Baja California Sur today. What is surprising is that no species of billfish other than *M. nigricans* has been positively identified in fossil deposits bordering the eastern North Pacific even though other Recent istiophorids (especially *I. platypterus* and *M. indica,* and *T. audax*) now inhabit the same waters at least during part of the year [Gottfried (1982) identified *I. platypterus* in the upper Pliocene San Diego Formation based on a fragmentary vertebra, but after examination of the specimen we believe it should be identified as Istiophoridae genus and species indeterminate]. Perhaps the absence of other istiophorids as fossils in the eastern North Pacific realm is due in part to our inability to accurately identify billfish from partial remains. Identifications are based primarily on comparing rostral fragments with complete rostra from Recent fish where emphasis is placed on cross-sectional morphology at 0.25L and 0.5L, two areas that must be estimated in fossil fragments. Fierstine and Voigt (1996) noted another limitation in their statistical study of rostra of Recent billfish; the lack of large-sized *M. nigricans* and *M. indica.* Species identifications of Recent billfish from vertebrae and other bones are based on small sample sizes as well (Fierstine 1998, 2001) and in most cases have not proven to be diagnostic (except for the predentary).

As noted above, Martínez-Gutiérrez and Sethi (1997) concluded that the middle facies (subunits B and C) of the Trinidad Formation were deposited in "shelf depths slightly greater than normal wave base", but that we concluded that the middle facies was deposited in much deeper water based on type of sediments. Because *M. nigricans* favors depths of over 100 m (Nakamura 1983, 1985), its presence in the Trinidad Formation supports a greater water depth and more open-sea environment, assuming that fossil and Recent blue marlin have similar ecological preferences. Two of the specimens, a predentary (IGM 7885) and a rostral fragment (IGM 7893), are badly eroded (possibly by stomach acid) and may have been transported into the San José del Cabo Basin as stomach contents of a more shallow-dwelling animal.

Acknowledgments

We thank M. del Carmen Perrilliat (IGM) and R. Feeney (LACM) for loan of specimens, F.S. Vernacchia (San Luis Diagnostic Center) for computer tomography (CT) images at minimal cost, and L.G. Barnes (LACM) for references and sage advice. Figure 3 was modified from an illustration by C. Bloomer. A. Fierstine provided encouragement throughout the study.

Literature Cited

Barnes, L.G. 1998. The sequence of fossil marine mammal assemblages in México. Avances en investigación. Paleontología de vertebrados. Universidad Autonoma del Estado de Hildago. Instituto de Investigaciones en Ciencias de la Tierra. Publicación Especial 1:26–79.

Berggren, W.A., D.V. Kent, C.C. Swisher, III, and M-P Aubry. 1995. A revised Cenozoic geochronology and chronostratigraphy. Pp. 129–212 *in* (W.A. Berggren, D.V. Kent, M-P Aubry, and J. Hardenbol eds.), Geochronology, time scales and global stratigraphic correlation. Soc. of Sedimentary Geol., Special publication 54.

Carpenter, K.E., B.B. Collette, and J.L. Russo. 1995. Unstable and stable classifications of scombroid fishes. Bull. Marine Sci., 56:379–405.

Carreño, A.L. 1992. Neogene microfossils from the Santiago diatomite, Baja California Sur, Mexico. Paleontología Mexicana, 59:1–37.

Davie, P. 1990. Pacific marlins: anatomy and physiology. Massey Univ. Press, Palmerston North, New Zealand, vii + 88 pp.

Espinosa-Arrubarrena, L. 1979. Los Tiburones fósiles (Lamniformes) del rancho Los Algodones, Baja California Sur, México. 60 pp. Tesis Profesional, Facultad de Ciencias, Universidad Nacional Autónoma de México.

Espinosa-Arrubarrena, L. and S.P. Applegate. 1981. Selacifauna Pliocenica de Baja California Sur, México y sus problemas de correlación regional. Pp. 667–681 *in* (Y.T. Sanguinetti, ed.), Anals del II Congreso Latino-Americano de Paleontología, Porto Alegre, Abril 1981.

Fierstine, H.L. 1998. *Makaira* sp., cf. *M. nigricans* Lacépède, 1802 (Teleostei: Perciformes: Istiophoridae) from the Eastover Formation, late Miocene, Virginia, and a reexamination of †*Istiophorus calvertensis* Berry, 1917. J. Vert. Paleo., 18:30–42.

Fierstine, H.L. 1999. *Makaira* sp., cf. *M. nigricans* Lacépède, 1802 (Teleostei: Perciformes: Istiophoridae) from the late Miocene, Panama, and its probable use of the Panama Seaway. J. Vert. Paleo., 19(3):430–437.

Fierstine, H.L. 2001. Analysis and new records of billfish (Teleostei: Perciformes: Istiophoridae) from the Yorktown Formation, Early Pliocene of eastern North Carolina at Lee Creek Mine. *in* (C.E. Ray and D.J. Bohaska, eds.), Geology and paleontology of the Lee Creek Mine, North Carolina, III. Smithsonian Cont. to Paleobiol.

Fierstine, H.L. and S.P. Applegate. 1968. Billfish remains from southern California with remarks on the importance of the predentary bone. Bull. South. Calif. Acad. Sci., 67(1):29–39.

Fierstine, H.L. and O. Crimmen. 1996. Two erroneous, commonly cited examples of "swordfish" piercing wooden ships. Copeia, 1996(2):472–475.

Fierstine, H.L. and N. Voigt. 1996. Use of rostral characters for identifying adult billfishes (Teleostei: Perciformes: Istiophoridae and Xiphiidae). Copeia, 1996(1):148–161.

Fierstine, H.L. and B.J. Welton. 1988. A late Miocene marlin, *Makaira* sp. (Perciformes, Osteichthyes) from San Diego County, California, U.S.A. Tertiary Research, 10(1):13–19.

Fletcher, J.M., B.P. Kohn, D.A. Foster, and A.J.W. Gleadow. Heterogenous Neogene cooling and exhumation of the Los Cabos block, southern Baja California: Evidence from fission-track thermochronology. Geology, 28(2):107–110.

Gottfried, M.D. 1982. A Pliocene sailfish *Istiophorus platypterus* (Shaw and Nodder, 1791) from southern California. J. Vert. Paleo., 2(2):151–153.

Gregory, W.K. and G.M. Conrad. 1937. The comparative osteology of the swordfish (*Xiphias*) and the sailfish (*Istiophorus*). Amer. Mus. Novitates, 952:1–25.

Hopper, C.N. 1986. The majestic marlin solves mysteries of the sea. Pp. 58–61, 63, 65–66, 68–70 *in* World Record Game Fishes 1986. International Game Fish Association, Fort Lauderdale, Florida.

Johnson, G.D. and C. Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. Pp. 554–626 *in* (G.D. Johnson and W.D. Anderson, Jr., eds.), Proceedings of the symposium on phylogeny of Percomorpha, June 15–17, held in Charleston, South Carolina at the 70th annual meeting of the American Society of Ichthyologists and Herpetologists, Bull. Marine Sci., 52:1–629.

Lacépède, B.G.E. 1802. Histoire naturelle des poissons. 4:689–697.

Martínez-Gutiérrez, G. and P.S. Sethi. 1997. Miocene-Pleistocene sediments within the San José del Cabo Basin, Baja California Sur, Mexico. Pp. 141–166 *in* Pliocene carbonates and related facies flanking the Gulf of California, Baja California, Mexico. (M.E. Johnson and J. Ledesma-Vázquez, eds.), Geol. Soc. of Amer. Special Paper 318.

McCloy, C. 1984. Stratigraphy and Depositional History of the San José del Cabo Trough, Baja California Sur, México. Pp. 267–273 *in* Geology of the Baja California Peninsula: Pacific Section SEPM (Frizzell, V.A., Jr., ed.), vol 39.

McDougall, K., R.Z. Poore, and J. Matti. 1999. Age and paleoenvironment of the Imperial Formation near San Gorgonio Pass, Southern California. J. of Foraminiferal Res., 29(1):4–25.

Nakamura, I. 1983. Systematics of billfishes (Xiphiidae and Istiophoridae). Publ. Seto Marine Biol. Lab., 28:255–396.

Nakamura, I. 1985. An annotated and illustrated catalogue of marlins, sailfishes, spearfishes, and swordfishes known to date. Food and Agricultural Organization of the United Nations (FAO) Fisheries Synopsis, 125(5):1–65.

Nelson, J.S. 1994. Fishes of the world, 3rd ed. John Wiley and Sons, Inc., New York, xvii + 600 pp.

Potthoff, T., S. Kelley, and J.C. Javech. 1986. Cartilage and bone development in scombroid fishes. Fishery Bulletin, 84(3):647–678.

Rivas, L.G. 1953. The pineal apparatus of tunas and related scombrid fishes as a possible light receptor controlling phototactic movements. Bull. Marine Sci. of the Gulf and Caribbean, 3(3):168–180.

Rivas, L.G. 1975. Synopsis of biological data on blue marlin, *Makaira nigricans* Lacépède, 1802. Pp. 1–16 *in* Proceedings of the International Billfish Symposium Kailua-Kona, Hawaii, 9–12 August 1972 Part 3. Species Synopses. (R.S. Shomura and F. Williams, eds.), National Oceanic and Atmospheric Administration Technical Report. NMFS SSRF-675.

Robins, C.R. and D.P. deSylva. 1960. Descriptions and relationships of the longbill spearfish, *Tetrapturus pfluegeri,* based on western North Atlantic specimens. Bull. Marine Sci. of the Gulf and Caribbean, 10:383–413.

Schultz, O. 1987. Taxonomische Neugruppierung der Überfamilie Xiphioidea (Pisces, Osteichthyes). Annalen Naturhistorisches Museum Wien, Serie A, für Mineralogie und Petrographie, Geologie und Paläontologie, Anthropologie, und Prähistories, 89:95–202.

Smith, J.T. 1991. Cenozoic Marine Mollusks and Paleogeography of the Gulf of California. Pp. 637–666 *in* The Gulf and Peninsular Province of the California. (Dauphin, J.P., and B.R.T. Simoneit, eds.). American Association of Petroleum Geologists, Memoir 47.

Strasburg, D.W. 1969. Billfishes of the Central Pacific Ocean. U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Biological Laboratory, Honolulu, Hawaii, Circular 311:1–11.

Accepted for publication 28 January 2001.

Bull. Southern California Acad. Sci.
100(2), 2001, pp. 74–85

Contributions to the Life History of Adult Pacific Lamprey (*Lampetra tridentata*) in the Santa Clara River Of Southern California

Shawn D. Chase

Sonoma County Water Agency, P.O. Box 11628, Santa Rosa, CA 95401

Abstract.—Data on the relative abundance, seasonal timing, and size at entry into freshwater of upstream migrants were collected on a population of Pacific lamprey inhabiting the Santa Clara River. In addition, spent lamprey were also collected and provided information on the length, decrease in body length between entry into freshwater and spawning the following year, and the potential timing of spawning.

The number of Pacific lamprey counted in the fish ladder has ranged from 20 in 1997 to 908 in 1994 and was at least partially related to the length of time that the ladder was open. The upstream migration is regulated by streamflow, and has begun as early as mid December, and as late as mid March in the Santa Clara River. The entire lamprey migration period was sampled only once during the 1995 season and the upstream migration spanned an approximately three month period (late January through early May). Peak lamprey migration occurred in March of most years. Pacific lamprey captured in the upstream ladder averaged between 593 and 610 mm in length between 1994 and 1997 (range 485–800 mm).

Adult Pacific lamprey in the Santa Clara River apparently spend approximately one year in freshwater prior to spawning. During this time, lamprey do not feed. The average length of spent Pacific lamprey collected in the downstream trap ranged from 427 mm in 1995 to 446 mm in 1997 (overall range 355 to 610 mm). Based on the capture of spent Pacific lamprey in the downstream trap, spawning likely begins by late January in most years, and spawning may continue into April.

Anadromus Pacific lamprey (*Lampetra tridentata*) inhabit coastal rivers and streams from northern Baja California (Rio Santo Domingo) (Ruiz-Campos et al. 1997) to Alaska (Unalaska) (Moyle 1976). Although this species has received some attention from researchers in Canada (e.g., Beamish 1980), very little is known about the life history of Pacific lamprey in California rivers. An opportunity to collect information on adult life history of Pacific lamprey in southern California occurred during a study designed to monitor the performance of fish passage facilities at the Vern Freeman Diversion on the Santa Clara River. The Vern Freeman Diversion is operated by the United Water Conservation District (UWCD), which diverts water at Saticoy, approximately 16.8 kilometers inland from the Pacific Ocean. In 1991, the UWCD constructed the Freeman Diversion Improvement Project to improve the existing diversion. This action was taken at the direction of the State Water Resources Control Board to combat seawater intrusion in the Oxnard Coastal Plain aquifers. This intrusion results from overdraft of groundwater to supply water for irrigation, industry, and municipal uses.

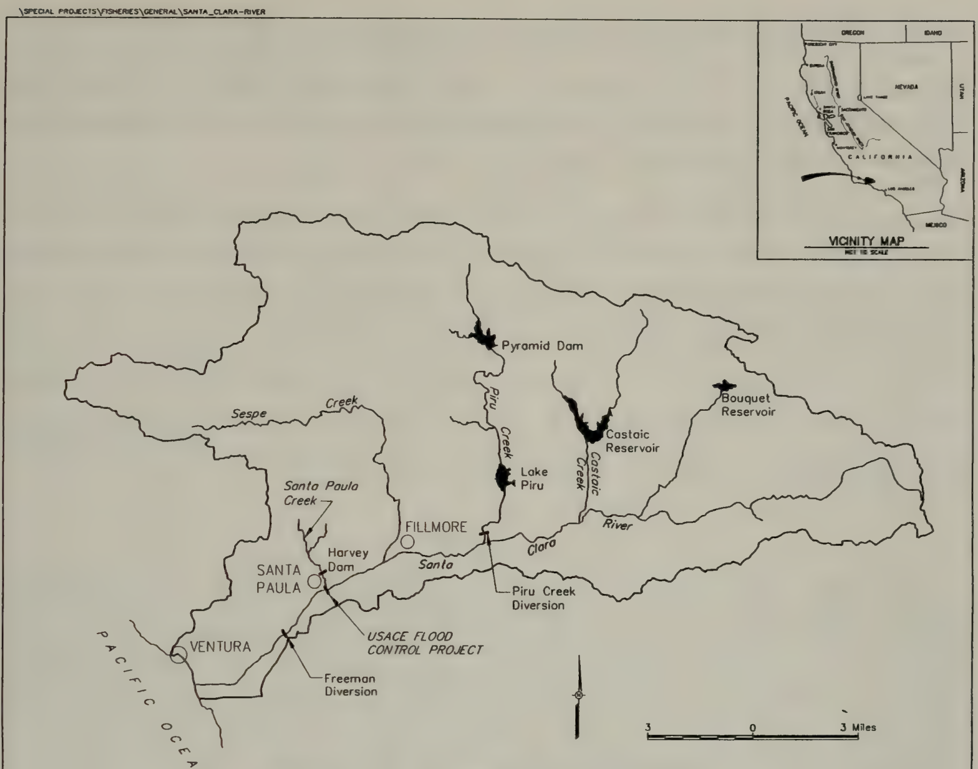

\SPECIAL PROJECTS\FISHERIES\GENERAL\SANTA_CLARA-RIVER
OREGON
IDAHO
NEVADA
UTAH
PACIFIC OCEAN
CALIFORNIA
ARIZONA
MEXICO
VICINITY MAP
NOT TO SCALE
Pyramid Dam
Piru Creek
Sespe Creek
Castaic Reservoir
Castaic Creek
Bouquet Reservoir
Lake Piru
Santa Paula Creek
FILLMORE
River
Clara
Santa
Harvey Dam
SANTA PAULA
Piru Creek Diversion
USACE FLOOD CONTROL PROJECT
VENTURA
Freeman Diversion
PACIFIC OCEAN
3
0
3 Miles

FIGURE 1: MAP OF SANTA CLARA RIVER BASIN

The improvements consist primarily of a permanent concrete riverbed stabilization structure and diversion. These were necessary for the UWCD to maintain its ability to divert water to groundwater recharge basins in the Oxnard Plain Forebay Basin. Historical in-river aggregate mining destabilized and degraded the Santa Clara River bed, which had lowered approximately 22 feet opposite the diversion headworks since 1928, when diversions began. The down cutting of the riverbed also contributed to repeated failures of the previous sand dike diversion structure. The permanent concrete structure, completed in 1991, has halted headcutting, stabilized the riverbed both upstream and downstream of the project, and improved the ability of UWCD to divert streamflow to groundwater recharge basins. The Freeman Diversion includes a two-entrance denil fish ladder, a fish screen, and by-pass facilities to provide anadromous fish passage upstream and downstream of the diversion facility.

Background

The Santa Clara River drains portions of Los Angeles and Ventura counties in southern California (Figure 1). The mainstem Santa Clara River flows through a narrow alluvial valley onto a coastal plain and is fed by several tributaries that flow out of local mountains. The major tributaries are Santa Paula, Sespe and Piru creeks. Streamflow is typical of most southern California rivers—extremely low to intermittent flow in its lower reaches during the dry summer and fall months, with high peak flows during winter storms. During the low flow period, a sand bar forms at the mouth of the Santa Clara River estuary forming an intermittent barrier to fish migration to or from the ocean. Fish also are prevented from migrating through the lower Santa Clara River until sufficient rainfall provides adequate streamflow to allow for passage.

The upper mainstem Santa Clara River provides habitat for several native species, including steelhead (*Oncorhynchus mykiss*), unarmored threespine stickleback (*Gasterosteus aculeatus williamsoni*), partially armored threespine stickleback (*G. a. microcephalus*), as well as the introduced Santa Ana sucker (*Catostomus santaanae*) and arroyo chub (*Gila orcutti*) (Bell 1978; Swift et al. 1993). The lower Santa Clara River (in the vicinity of the Vern Freeman Diversion Facility) serves primarily as a migration corridor for steelhead and lamprey (Puckett and Villa 1985). Spawning and rearing habitat for steelhead and Pacific lamprey are located primarily in upstream tributaries, such as Sespe Creek (Puckett and Villa 1985).

Methods

This study was designed to monitor the upstream (adult) and downstream (smolt) migrations of steelhead through the fish ladder and fish by-pass facility at the Vern Freeman Diversion (ENTRIX 1991). In 1991, a temporary trap and fyke net was placed in the ladder during a high flow event to monitor fish movement upstream through the diversion facility. In 1993, a semi-permanent fish trap was installed in the fish ladder. Under agreement with the California Department of Fish and Game, U. S. Fish and Wildlife Service and the U. S. Army Corp of Engineers (USACE), the fish ladder will be operated throughout the upstream migration period in the Santa Clara River at the Vern Freeman Diversion provided certain criteria were met (detailed in the USACE Section 404 Permit). The ladder may be closed 48 hours after streamflow (above the diversion) has declined below 415 cfs. The diversion facility is not operated under extremely high streamflow conditions and when turbidity levels exceed approximately 2,000 NTU's. The ladder is also closed temporarily when sand is flushed from the mouth of the diversion intake. The downstream by-pass facility is operated as long as there is continuous flow to the ocean. When flow is discontinuous, smolts are collected in a trap and transported to the estuary/ocean for release, depending upon the condition (open or closed) of the estuary's mouth.

Upstream Trap

A denil-type fish ladder provides access for upstream migrating fish around the diversion structure. During periods of high streamflow, a relatively high velocity current is required to attract upstream migrating steelhead into the fish ladder. The water surface elevation inside the fish ladder (at the downstream fish entrance) is maintained such that the head created by this elevational difference results in a mean water velocity flowing out of the fish ladder at a calculated eight feet per second.

The trap was serviced every morning that the ladder was in operation. During servicing, the fish ladder was drained by closing the upstream gates and debris and sand that collected around the trap were removed. The fish trap was checked during this time. In addition, the rest of the fish ladder was surveyed for fish stranded between the baffles as a result of the dewatering of the fish ladder.

Pacific lamprey collected in the ladder were counted and measured to the nearest centimeter, total length (TL). Photographs were taken of representative individuals. Lamprey were then released upstream of the trap to continue their upstream migration.

In 1994 and 1995, a marking study was conducted to determine if adult Pacific lamprey required more than one 24-hour period to ascend the fish ladder. In each year, 100 adult lamprey were marked with a hole-punch in the dorsal fin and released back into the ladder where they were originally found. The number of lamprey with hole-punched dorsal fins were recorded on the day following the marking event.

Downstream Trap

Adult lamprey were collected in the downstream trap and in the diversion canal, upstream of the fish screens. Lamprey collected in the downstream trap were counted, measured, and released into the fish by-pass facility (essentially a pipe leading back to the river downstream of the diversion facility). The diversion's intake is located near the outlet of the fish ladder. Therefore, it was possible for upstream migrating lamprey to be swept back into the diversion and into the downstream trap (however, the occurrence of upstream migrants in the downstream trap was extremely low). Upstream migrants and spent Pacific lamprey were distinguished based on the presence or absence of abrasions and lesions. Pacific lamprey were classified as spent adults if they were covered with abrasions (assumed to be the result of constructing redds). Lamprey lacking abrasions were classified as upstream migrants that were swept back into the diversion canal.

Results

Timing of Upstream Migration

Since streamflow in the Santa Clara River is intermittent during the long dry summer period, streamflow conditions suitable for upstream migration are solely dependent on winter rains. The length of time that anadromous fish have to migrate through the lower Santa Clara River is controlled by the timing and intensity of rainfall, and by the operations rules for the fish ladder and diversion.

Rainfall varied greatly in the project area during the years sampled. Rainfall data have been collected in Santa Paula (located approximately 10 miles east of the diversion) since 1890. Since 1890, annual rainfall in the basin has ranged from 6.42 to 38.11 inches, averaging 17.28 inches. Between 1994 and 1997, annual rainfall totals have ranged from 13.39 to 35.34 inches. The length of time that streamflow conditions suitable for upstream migration existed ranged from 29 days in 1996 to 137 days in 1995.

In 1994, rainfall totaled 13.39 inches (65 percent exceedance). The sand bar at the mouth of the river likely first breached on 7 February, and streamflow conditions suitable for upstream migration existed in the lower river until 9 April (62 days) (Table 1, Figure 2). Upstream migrating Pacific lamprey were observed in the ladder from 17 February through 9 April, when the ladder was closed according to 404 Permit conditions. The number of lamprey observed in the ladder was relatively low during the first four weeks that the ladder was operated (61

Table 1. Probable date of breaching of the stream mouth and recording of first lamprey in ladder.

Year	Probable date sand bar breached	Date first lamprey in ladder	Last day lamprey recorded	No. of days ladder operated
1994	7 February	17 February	9 April[1]	50
1995	2 January	18 January	18 May	137
1996	20 February	25 February	25 March[1]	23
1997	24 December[2]	16 December	18 February[1]	45

[1] Ladder likely closed prior to the end of the upstream migration period.

[2] Sand bar breached briefly in October, November, and early December for a few days at a time prior to the 24 December breaching event.

total by March 15). On March 16, 142 lamprey were counted in the ladder, the highest single daily total during the study. During the last two weeks of March, 676 adult lamprey were counted. A total of 908 adult Pacific lamprey were observed in the ladder during 1994 (Table 2).

In 1995, rainfall totaled 35.34 inches (4 percent exceedance). The sand bar at the mouth of the river likely first breached on 2 January, and suitable streamflow conditions for upstream migration existed in the lower river through 20 May (137 days). Pacific lamprey were observed in the ladder from 18 January through 18

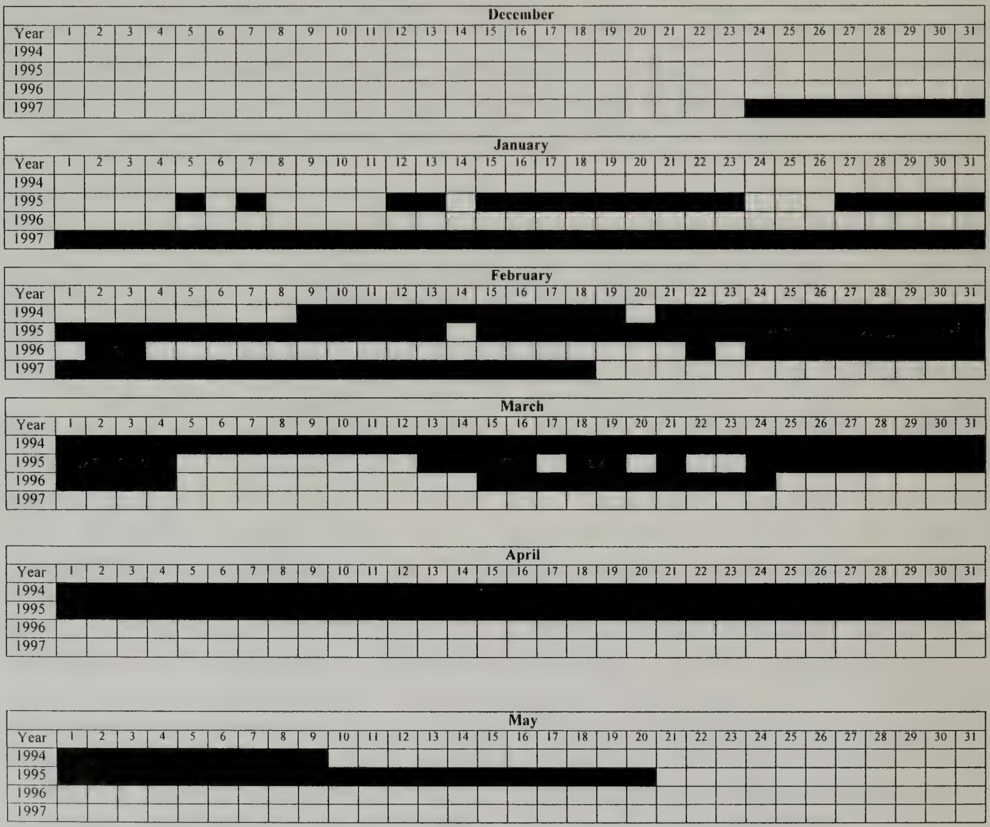


Fig. 2. Dates that the Upstream fish ladder was in operation, 1994–1997.

Table 2. Weekly counts of adult Pacific lamprey caught in the upstream migrant trap, 1991–1997.

Month	Week ending	1991[1]	1993[2,3]	1994[4]	1995[5]	1996[6]	1997[7]
December	17	—	—	—	—	—	2
	24	—	—	—	—	—	1
January	7	—	—	—	0	—	0
	14	—		—	0	—	0
	21	—		—	1	—	1
	28	—		—	2	—	0
February	4	—	88	0	95	—	0
	11	—		0	74	—	1
	18	—		1	35	—	7
	25	—		19	16	14	8
March	4	—	318	11	24	85	—
	11	—		7	2	19	—
	18	—		283	4	36	—
	25	—		240	20	155	—
April	1	74	48	201	20	—	—
	8	—		133	34	—	—
	15	—		13	9	—	—
	22	—		—	9	—	—
	29	—		—	3	—	—
May	6	—	11	—	13	—	—
	13	—		—	8	—	—
	20	—		—	2	—	—
	27	—		—	—	—	—
June	4	—		—	—	—	—
	11	—		—	—	—	—
Total		74	465	908	368	309	20

[1] Ladder operated from 26 March to 2 April, 1991.

[2] Ladder operated from 17 February to 17 May, 1993.

[3] Daily lamprey counts were visually estimated on some days during 1993 (e.g., "15 to 20 lamprey in ladder today"), on these days the lower value was used to estimate abundance, and the numbers were combined into monthly totals only.

[4] Ladder operated from 4 February through 9 April, 1994.

[5] Ladder operated from 6 January through 20 May, 1995.

[6] Ladder operated on 2–3 February, from 22 February through 5 March, and from 14 through 25 March, 1996.

[7] Includes leap year day (8 day period).

May (Table 1). Prior to 31 January, three lamprey were observed in the ladder. Approximately 46 percent of the Pacific lamprey run occurred during the first two weeks of February. The lamprey migration remained fairly constant through the second week in April. In 1995, 368 adult Pacific lamprey were observed in the ladder (Table 2).

In 1996, rainfall totaled 13.90 inches (59 percent exceedance). Significant rainfall during this year did not fall in southern California until February, and the sand bar at the mouth of the river likely first breached on 20 February. Adult Pacific lamprey were first observed in the ladder on 25 February. Suitable flow conditions for upstream migration existed in the lower river from 25 February through 5 March, and again from 14 March through 25 March (29 days) (the ladder was closed between 6 March and 13 March). Weekly counts of lamprey

Table 3. Minimum, maximum and average lengths (mm) of upstream migrating Pacific lamprey, 1994–1996.

Year	Minimum length	Maximum length	Average length	N
1994	535	700	610	71
1995	485	750	610	254
1996	490	675	604	232
1997	512	800	593	19

peaked during the last week that the ladder was open. A total of 309 adult Pacific lamprey were observed in the ladder during 1996.

In 1997, rainfall totaled 19.64 inches (31 percent exceedance), falling primarily during December and January. The sand bar at the mouth of the river likely first breached in October for a short time-period, and again in November and early December. The sand bar breached again on 24 December with suitable flow conditions for upstream migration existed in the lower river until 18 February (57 days). Adults were observed in the fish ladder from 16 December, after one of the brief breaching events, and a few lamprey were counted in the ladder through 18 February, when the ladder was closed. Although suitable streamflow conditions were present to allow for upstream migration during December and January, only four lamprey were observed in the ladder during this time. A total of 20 adult Pacific lamprey were observed in the ladder during 1997 (Table 2).

Counts

Counts of Pacific lamprey in the ladder represent a minimum number of migrating adults since the trap probably does not hinder upstream movement. Marking studies conducted in 1994 and 1995 found that the majority (92 and 93 percent, respectively) of the lamprey were able to negotiate the fish ladder in less than 24 hours. The number of adult Pacific lamprey recorded in the ladder annually has ranged from 20 (1997) to 908 (1994). However, the entire run was censused only once, in 1995, when 371 adult lamprey were counted (Table 2). In 1993, sampling began after lamprey were first observed in the ladder, when 465 adult lamprey were counted.

Length of Adults at Time of Entry into the River

The upstream migrating lamprey ranged in total length (TL) from 485 to 800 mm (Table 3). The average length of upstream migrating Pacific lamprey has been nearly constant. Pacific lamprey averaged 610 mm TL in 1994 and 1995, 604 mm TL in 1996, and 593 mm TL in 1997.

Likely Time of Spawning

Adult lamprey in a variety of conditions ranging from dead to apparently healthy and vigorous have been captured in the downstream trap. The majority of these lamprey were covered with abrasions, and were assumed to have recently spawned. Timing of spent lamprey appearing in the downstream trap is related to the onset of spawning and very likely streamflow in spawning tributary(s) and in the Santa Clara River. It is not known how long after spawning that lamprey weaken to the point where they begin to drift downstream, or how long it takes

Table 4. Weekly summary of adult Pacific lamprey caught in the downstream migrant trap, 1994–1996.

Month	Week Ending	1994[1]	1995[2]	1996[3]	1997[4]
January	7	—	0	—	—
	14	—	0	—	—
	21	—	0	—	—
	28	—	0	—	—
February	4	0	2	—	—
	11	0	3	0	1
	18	0	1	1	0
	25	0	0	5	1
March	4	0	2	2	3
	11	2	1	0	4
	18	18	1	2	4
	25	20	0	18	2
April	1	13	10	12	1
	8	10	6	5	1
	15	5	4	2	—
	22	0	8	3	—
	29	0	18	4	—
May	6	1	32	0	—
	13	1	5	—	—
	20	0	3	—	—
	27	—	5	—	—
June	3	—	9	—	—
	10	—	3	—	—
	17	—	0	—	—
	24	—	0	—	—
July	1	—	0	—	—
	8	—	0	—	—
	15	—	0	—	—
	22	—	0	—	—
Total		70	113	54	17

[1] Downstream trap closed on 25 May, 1994.
[2] Downstream trap closed on 27 July, 1995.
[3] Downstream trap closed on 3 May, 1996.
[4] Downstream trap closed on 29 April, 1997.

Table 5. Number, seasonal timing, and lengths of Pacific lamprey captured in the downstream trap between 1994 and 1996.

Year	Number	First observed	Last observed	Range	Average length
1994	25	10 March	21 May	390–479	441
1995	103	4 February	11 June	355–510	427
1996	54	17 February	29 April	355–615	438
1997	16	10 February	8 April	411–492	446

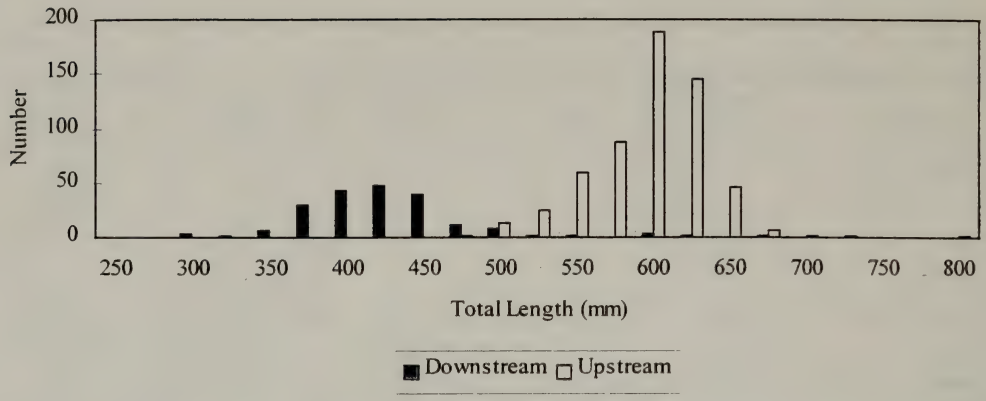


Fig. 3. Length-frequency of Pacific lamprey collected in the upstream and downstream fish by-pass facilities, 1994–1997 data combined.

them to drift from spawning tributaries down to the diversion dam. Spent lamprey have been collected from 4 February to 11 June (Tables 4 and 5). Spent lamprey occurrence in the downstream trap peaked in late March and early April during 1994 and 1996 and in May during 1995 (Table 4). Based on the capture of spent lamprey in the trap, spawning begins in late January and may continue through at least May in some years. Peak spawning probably occurred between February and April.

Length of Pacific Lamprey Collected in the Downstream Trap

Pacific lamprey collected in the downstream trap ranged in length between 355 and 615 mm TL between 1994 and 1997 (Table 5). Similar to lamprey collected in the upstream trap, the average length of lamprey collected in the downstream trap remained relatively constant between years, ranging from 427 to 446 mm TL between 1994 and 1997.

Decrease in Body Length Between Entry into Freshwater and After Spawning

Pacific lamprey collected in the upstream trap were considerably larger compared to lamprey collected in the downstream trap within the same year (Figure 3). I hypothesize that the lamprey collected in the downstream trap are members of the previous year's upstream migration as has been previously described by Beamish (1980). If this hypothesis is correct, then Pacific lamprey in the Santa

Table 6. A comparison of total body lengths of adult Pacific lamprey at the time of upstream migration and after spawning the following year.

	Average length (mm)	Range (mm)	Difference (mm)	Percentage decrease
Pre-spawn length in 1994	610	485–750		
Post spawn length in 1995	427	355–508	183	30.0
Pre-spawn length in 1995	610	485–750		
Post spawn length in 1996	437	355–615	173	28.2
Pre-spawn length in 1996	604	490–675		
Post spawn length in 1997	446	411–492	158	26.2

Clara River decreased in body length, on average, between 26.2 and 30.0 percent of their body length between entry into freshwater and spawning (Table 6). The alternative hypothesis that the lamprey captured in the downstream trap are members of that year's spawning migration would require that the observed decrease in body length would have occurred over a relatively short (one to three month) period.

Discussion

Timing of Upstream Migration

Migration in the Santa Clara River is regulated by streamflow, and adult lamprey have been observed in the ladder for the first time as early as mid-December in 1997 and as a late as the last week in March in 1991, depending on the timing of winter rains. Adult lamprey are not thought to range far from their natal streams during the marine phase of their life history (Moyle 1976). Lamprey have been collected in the fish ladder (approximately 16.8 kilometers inland) as early as six days after the probable breaching date of the lagoon mouth, and as late as 16 days after the lagoon breached. However, the number of adult lamprey captured in the ladder have typically remained low during the first two weeks of the run.

In California, Pacific lamprey have been reported to migrate upstream between April and late July (Moyle 1976; Wang 1986), although in the Trinity River in northern California, Moffett and Smith (1950, cited by Moyle 1976) reported upstream migration by adult lamprey in August and September. In the Santa Clara River, upstream migrating Pacific lamprey were observed from mid-December through mid-May between 1994 and 1997. However, the peak run generally occurred between February and the first week of April. The adult Pacific lamprey upstream migration period spanned an approximately four-month period (mid-January though mid-May) in 1995, the only year to date that the entire lamprey spawning migration was sampled. However, 87.3 percent of the run was observed in the ladder between February and the first week of April. Very few Pacific lamprey were observed in the ladder prior to February in any year. For example, in 1997, although suitable streamflows for migration were present from late December through January, five lamprey were observed in the ladder during this time. The upstream migration period extended into the first week of May in 1993 and the third week in May in 1995. The apparent earlier timing of upstream migration in the Santa Clara River, compared to more northern river systems, is likely an adaptation to the rainfall pattern in southern California, where the majority of the precipitation, and thus suitable streamflow conditions, occur between January and March.

The number of Pacific lamprey counted in the fish ladder has ranged from a low of 20 in 1997 to 908 in 1994. The numbers of lamprey counted at the Vern Freeman Diversion represent a minimum number; the true number of lamprey returning to the river is undoubtedly higher. Pacific lamprey can pass through the ladder unhindered. Thus an unknown number of adult lamprey could migrate through the fish ladder without being detected. A test using a mark-recapture technique demonstrated that slightly more than 90 percent of the lamprey could pass through the ladder in less than 24 hours.

Size at Time of Upstream Migration

Upstream migrating lamprey collected in the fish ladder ranged from 485 to 800 mm TL, averaging approximately 606 mm TL between 1994 and 1997. Pacific lamprey in the Santa Clara River are comparable in length to those collected in Canada. In Canada, upstream migrating lamprey ranged in length between 130 and 720 mm TL in six populations reported by Beamish (1980). These populations could be divided into two size ranges based on length; a "small" population averaging between 260 and 290 mm in length (ranging between 130 and 510 mm in length for three populations combined), and a "large" group averaging between 600 and 640 mm TL (ranging between 550 and 720 mm in length for three populations combined) (Beamish 1980).

Pacific lamprey do not feed after reentering freshwater during their spawning migration (Hardisty and Potter 1971; Whyte et al. 1993). Energy reserves are used for migrating to natal spawning areas and gonadal development. During this period of starvation, Pacific lamprey decrease in length and weight (Hardisty and Potter 1993). Pacific lamprey have been kept alive under laboratory conditions for up to two years without eating (Whyte et al. 1993). A similar decrease in body length was observed in lamprey in the Santa Clara River. Between 1994 and 1997, Pacific lamprey collected in the downstream trap averaged 427 and 446 mm TL, compared to Pacific lamprey captured in the upstream trap which averaged 593 and 610 mm TL. Hardisty and Potter (1993) and Beamish (1980) have reported that lamprey may remain in fresh water for approximately one year prior to spawning. Based on the differences in the average size of Pacific lamprey collected in the upstream and downstream traps, combined with the peak occurrences of lamprey in the two facilities, it appears that Pacific lamprey in the Santa Clara River hold over in fresh water for one year prior to spawning. If the smaller lamprey captured in the downstream trap are members of the previous years spawning migration, then adult lamprey decreased, on average, between 26.2 and 30.0 percent of their body length between entering freshwater and spawning the following year. Since peak abundance of lamprey in the upstream and downstream fish passage facilities occurred at approximately the same time (between late February and early May), the observed difference in body length would have had to occurred over an approximately one to two month period for the lamprey collected in the downstream trap to have been part of that years upstream migration. In addition, in 1996, the first lamprey was observed in the downstream fish by-pass facility on 17 February, although the mouth of the lagoon was first breached on or about 19 February. A similar decrease in body length was reported for Pacific lamprey inhabiting rivers in British Columbia. Beamish (1980) reported that Pacific lamprey decreased in length at least 20 percent between the time of entry into freshwater and the on-set of spawning. However, the lamprey in Beamish's study had been in freshwater for an unknown period of time, and thus the actual length at time of entry was unknown.

Pacific lamprey have been reported to die after spawning (Hardisty and Potter 1971), although, Michaels (1980, 1984) reported that some lamprey survived to spawn again a second time. Some of the spent lamprey captured in the downstream trap were still alive at the time of capture. It is not known if any were able to successfully readapt to a saltwater existence and survive to spawn a second time.

Based on the capture of spent lamprey in the downstream trap in 1995 between 4 February and 11 June, it appears that spawning may begin as early as January and may continue into at least May. In 1996, a relatively dry year, spent lamprey were captured in the downstream trap between 17 February and 28 April.

This time period suggests that Pacific lamprey spawn earlier in the Santa Clara River compared to more northern rivers, where spawning has been reported to occur between April and July (e.g. Moyle 1976, Beemish, 1980, Wang 1986). As with the earlier timing of upstream migration, the earlier spawning period for Santa Clara River lamprey is likely an adaptation to the timing of precipitation in southern California.

Acknowledgments

The United Water Conservation District provided the funding for this study. John Dickenson, UWCD Project Engineer, allowed and encouraged the collection of data outside the scope of the 404 permit requirements. Wayne Lifton contributed significantly to the development of the original study plan and in the editing of the annual reports that formed the basis of this report. John Southwick collected and measured most of the lamprey for this study, and without his dilengent efforts, this study would not have been possible. The Author also wishes to thank Drs. Richard Beamish, Peter Moyle, and Camm Swift for their thoughtful review of this paper. Their comments and insights are greatly appreciated.

Literature Cited

Beamish, R. J. 1980. Adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. Canadian Journal of Fish and Aquatic Sciences. 37:1906–1923.

Bell, M. A. 1978. Fishes of the Santa Clara River System, southern California. Contributions in Science. Natural History Museum of Los Angeles. 295:1–20.

ENTRIX Inc., 1991. Vern Freeman Diversion Project fishery mitigation monitoring study plan to address 404 permit special condition B. Prepared for the United Water Conservation District. 15 pp.

Hardisty, M. W. and I. C. Potter. 1971. The General Biology of Adult Lampreys. *In* Hardisty and Potter, eds. The Biology of Lampreys. Volume 1. Academic Press London.

Michael, J. H., Jr. 1980. Repeat spawning of Pacific lamprey. California Fish and Game. 66(3): 186–187.

Michael, J. H., Jr. 1982. Additional notes on the repeat spawning by Pacific lamprey. California Fish and Game. 66(3): 186–187.

Moffett, J. W. and S. H. Smith. 1950. Biological investigations of fisheries resources of Trinity River, California. USFWS Spec. Sci. Rep. Fisheries 12:71 pp.

Moyle, P. B. 1976. Inland fishes of California. University of California Press, Berkeley. 405 pp.

Puckett, L. K. and N. A. Villa. 1985. Lower Santa Clara River Steelhead Study: Final Report. Department of Fish and Game. 31 pp.

Ruiz-Campos, G., S. Contreras-Balderas, M. L. Lozano-Vilano, S. Gonzales-Guzman, and J Alaniz-Garcia. 1997. Distributional status of the continental fishes of the northwester Baja California, Mexico. 1996 Desert Fishes Council Proceedings.

Wang, J. C. S. 1986. Fishes of the Sacramento-San Joaquin Estuary and adjacent waters, California: a guide to the early life histories. Prepared for the Interagency Ecology Study Program for the Sacramento-San Joaquin Estuary. Technical report 9.

Whyte, J. N., R. J. Beamish, N. G. Ginther, and C.-E. Neville. 1993. Nutritional condition of the Pacific lamprey (*Lampetra tridentata*) deprived of food for periods of up to two years.

Accepted for publication 17 September 2000.

Bull. Southern California Acad. Sci.
100(2), 2001, pp. 86–95

Combined Effects of Drought and *Phoradendron juniperinum* Infestation Severity on Fruit Characteristics of *P. juniperinum* and its *Juniperus osteosperma* Hosts

Simon A. Lei

Department of Biology, WDB, Community College of Southern Nevada,
6375 West Charleston Boulevard, Las Vegas, Nevada 89146-1139

Abstract.—The interactive effects of severe drought and severity of *Phoradendron juniperinum* (juniper mistletoe) infestation on fruit characteristics of parasitic *P. juniperinum* and its *Juniperus osteosperma* (Utah juniper) host trees were examined in Pine Creek of the Red Rock Canyon National Conservation Area in southern Nevada. A severe drought, characterized by extremely low precipitation and above average air temperatures, started in January and persisted through mid-July 1997. Significant interactions were detected between drought and parasite severity for fruit production, fruit water content, diameter, thickness, dry mass as well as seed length and seed dry mass of *P. juniperinum.* Similarly, significant ineractions were found between drought and parasite severity for fruit and seed characteristics of *J. osteosperma* hosts. There was also evidence for significant correlations between the drought* parasite severity combination and all of the fruit traits measured in both hosts and parasites, and evidence for more positive correlations with parasites as the severity of drought increased in Pine Creek.

Phoradendron juniperinum (juniper mistletoe) are autotrophic hemiparasites inhabiting branches of higher vascular plants (Kuijt 1969; and Calder and Bernardt 1983). These parasites are photosynthetic but show some physiological dependence on a host plant, and use the xylem sap of the host to provide water and mineral nutrients (Calder and Bernhardt 1983). *Phoradendron juniperinum* are parasitic on woody plant species that are sparsely distributed in southern Nevada. These parasites commonly grow on *Juniperus osteosperma* (Utah juniper) and other gymnosperm hosts (Munz 1974). The final outcome is a net gain in *P. juniperinum* foliage, which occupies more and more of the host canopy as the infection intensifies through time (Calder and Bernhardt 1983).

Drought refers to a period with low precipitation in which the water content of the soil greatly reduces and the plants suffer from lack of water. The warm Mojave Desert of southern Nevada is permanently arid, with annual precipitation amounts of less than 105 mm (NOAA, Las Vegas and vicinity). Precipitation variability is a major factor in the occurrence of drought. Southern Nevada experienced an extreme drought during the first six months of 1997, with precipitation falling well below the monthly averages (NOAA, Las Vegas and vicinity). Moreover, the severity of the drought increased with decreasing elevation. Infestation of *P. juniperinum* greatly reduces host growth and the ability to survive drought and insect outbreak (Calder and Bernhardt 1983), particularly in juvenile host trees. Damage to host plants is largely caused by a combination of environmental and *Phoradendron*-induced water and nutrient (physiological) stress (Hollinger 1983; Glatzel 1983; Schulze and Ehleringer 1984; Schulze et al. 1984; Ehleringer et al. 1986). From casual observations, the fruit production and other fruit traits of *P. juniperinum* and its *J. osteosperma* hosts appeared to be greatly reduced by drought in southern Nevada.

The biology of *P. juniperinum* and its *J. osteosperma* host trees is well documented (Kuijt 1969; Calder and Bernhardt 1983; Schulze and Ehleringer 1984; Ehleringer et al. 1986; Dawson et al. 1990). *Juniperus osteosperma* hosts serve as both habitat and resource (water and nutrients) for parasitic *P. juniperinum.* Yet, possible interactions and correlations between drought and severity of *P. juniperinum* infestation in determining the fruit characteristics of both *J. osteosperma* hosts and *P. juniperinum* have not been documented. Two hypotheses were made prior to data collection. First, effects of drought or effects of *P. juniperinum* infestation would adversely impact various fruit characteristics of both *J. osteosperma* hosts and parasitic *P. juniperinum* plants. Second, there would be interactions and correlations between the drought* parasite severity combination and fruit traits of both hosts and parasites, and more positive correlations with the parasites. These two hypotheses were tested by a combination of field and laboratory measurements of various fruit traits with appropriate statistical analyses.

Materials and Methods

Study Site and Field Surveys

Pine Creek of the Red Rock National Conservation Area (36°05′ N, 115°40′ W; elevation 1,400 m) in the Spring Mountains was selected on the basis of *P. juniperinum–J. osteosperma* interactions during summers of 1997 and 1998. Winters and springs of 1997 and 1998 represented drought and non-drought periods, respectively (Fig. 1). Precipitation was 75.8 % lower during the first six months of the 1997 drought compared to 1998. The drought was ended by above average monsoonal rainfalls in July and September of 1997. Well above average rainfalls associated with an El Nino Southern Oscillation (ENSO) event occurred in Winter and early Spring of 1998 (Fig. 1). Mean monthly air temperatures varied considerably during the first six month of drought (1997) and non-drought (1998) periods (Fig. 2).

A total of 85 *J. osteosperma* trees was found in Pine Creek, and these trees were surveyed for the presence of parasites. Thirty (30) of 85 trees were not infested by parasites. All 55 host trees infested with *P. juniperinum* were similar in size. From casual observations, various levels of *P. juniperinum* infestation were evident, and localized influences of *P. juniperinum* on its *J. osteosperma* hosts were conspicuous. The 55 *P. juniperinum*-infested trees were categorized into three levels (light, moderate, and heavy) of infestation. Light, moderate, and heavy infestation implied under 20, between 20 and 40, and over 40 *P. juniperinum* individuals per *J. osteosperma* tree, respectively.

Field and laboratory measurements of fruit characteristics were conducted twice: once in the drought and once in the non-drought period. Because some fruits of both host and parasitic plants may persist from one year to the next, all fruits were collected when counting. Fruits of the same plants were collected in early August of 1997 and 1998 to ensure comparability. Brightly colored flagging tapes were used to tag canopies of host and parasitic plants for ease of visuali-

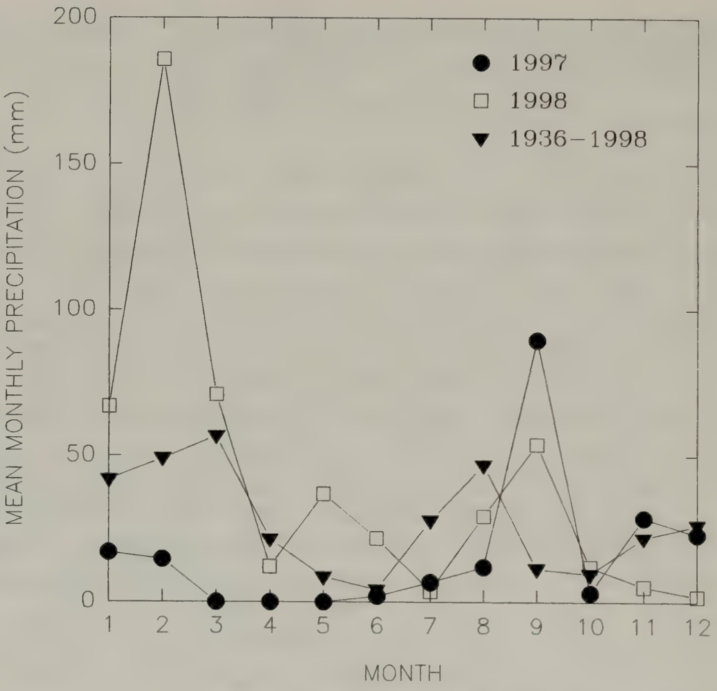


Fig. 1. Comparison of mean monthly precipitation among the 1997 (drought), 1998 (non-drought), and 1936–1998 (average) years (NOAA, Red Rock Canyon, elevation 1,400 m).

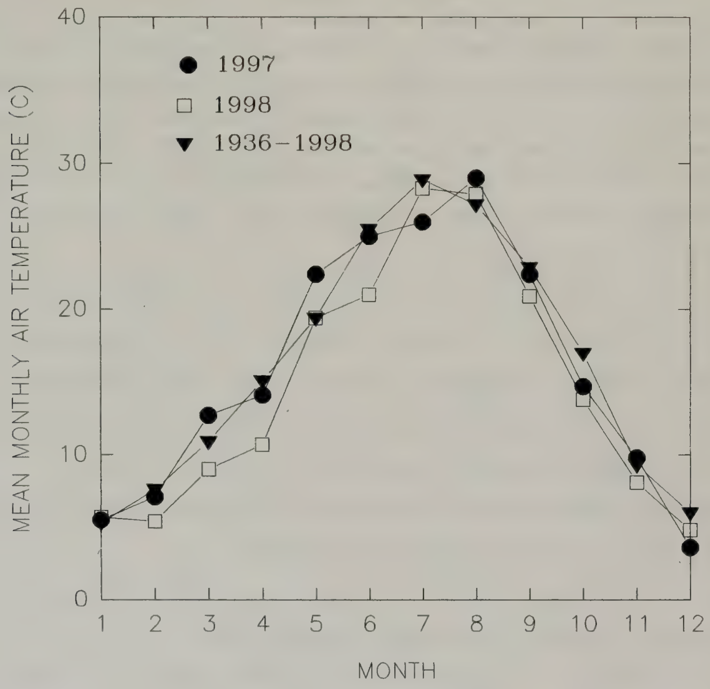


Fig. 2. Comparison of mean monthly air temperature among the 1997 (drought), 1998 (non-drought), and 1936–1998 (average) years (NOAA, Red Rock Canyon, elevation 1,400 m).

Table 1. Two-way ANOVA results of the effects of year, severity of infestation, and their interactions on various fruit characteristics of *P. juniperinum.* df = 1 for year; df = 2 for parasite severity and for year*parasite severity combination. Significance levels: *: $P \leq 0.05$; **: $P \leq 0.01$; ***: $P < 0.001$; ns: non-significant.

	Year		Parasite severity		Year*severity	
Fruit trait	F	P	F	P	F	P
Production	295.38	0.0034**	126.88	0.0078**	403.23	0.0002***
% water content	608.22	0.0016**	543.00	0.0018**	97.56	0.0019**
Diameter	144.27	0.0012**	82.45	0.0022**	176.58	0.0000***
Thickness	6.00	0.0917ns	10.50	0.0424*	20.00	0.0041**
Dry mass	13.36	0.0354*	7.55	0.0655ns	13.90	0.0091**
Seed length	2.54	0.2152ns	4.80	0.1151ns	7.19	0.0338*
Seed dry mass	75.00	0.0032**	10.00	0.0452*	72.50	0.002**

zation in the subsequent year. Fruit production was determined by counting the number of berries from individual *J. osteosperma* and *P. juniperinum* canopies during the peak or near peak fruit production. A total of 100 berries was randomly selected in each infection level of hosts and parasites to measure fruit dry mass, size (diameter and thickness), water content, as well as seed length and dry mass. Host trees included individuals with three levels parasitic infections, as well as individuals without any visible parasites (control) on trunks and branches.

Statistical Analyses

Two-way analysis of variance (ANOVA; Analytical Software 1994) was performed on fruit characteristics of parasitic *P. junierinum,* with year (drought and non-drought) and parasite severity (light, moderate, and heavy) as main effects. Similarly, two-way ANOVA was also performed on fruit characteristics of *J. osteosperma,* with year and parasite severity (control, light, moderate, and heavy) as main effects. In order to assess host and parasite plant responses to changes in weather condition, linear regression analysis was used to correlate fruit characteristics with year, parasite severity, and year* severity combination. Fruit water content was expressed in percentages. Mean values of fruit production and fruit water content were presented with standard errors, and statistical significance was determined at $P \leq 0.05$.

Results

Significant interactions ($P \leq 0.05$; Table 1, Figs. 3 and 4) were detected between year and severity of *P. juniperinum* infestation for all measured fruit characteristics of *P. juniperinum.* Between periods of high and low precipitation, significant differences ($P \leq 0.05$) were observed in fruit production (Fig. 3), fruit water content (Fig. 4), fruit diameter, fruit dry mass, as well as seed dry mass (Tables 1 and 3). Fruit production, fruit water content, diameter, thickness, as well as seed dry mass were also found to be significantly different ($P \leq 0.05$) among the three levels of infestation (Tables 1 and 3).

Significant correlations were also detected between all *P. juniperinum* fruit traits and year* parasite severity combination. Seed length was significantly correlated with year ($P \leq 0.05$; Table 2). Fruit thickness and dry mass were significantly correlated with parasite severity ($P \leq 0.05$; Table 2).

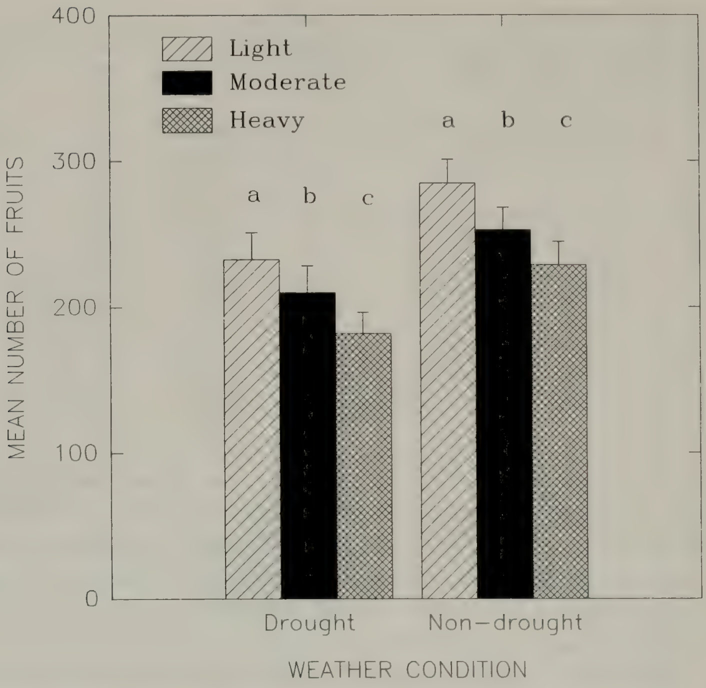


Fig. 3. Fruit production (Mean ± SE, n = 100 per treatment) of *P. juniperinum* growing on *J. osteosperma* hosts with three levels of infections in Pine creek of southern Nevada. Narrow vertical bars denote standard errors of the means. Within the same weather condition, columns labeled with different letters are significantly different at $P \leq 0.05$.

Significant interactions ($P \leq 0.05$; Table 4, Figs. 5 and 6) were observed between year and severity of infestation for all measured fruit traits of *J. osteosperma* hosts. Between the two years, significant differences were detected in fruit production (Fig. 5), fruit water content (Fig. 6), along with seed length and dry mass (Tables 4 and 6). Fruit production, fruit water content, and seed dry mass were found to be significantly different ($P \leq 0.05$) among the three levels of infestation.

Significant correlations were also seen between host fruit traits and year* parasite severity combination. Seed dry mass was significantly ($P \leq 0.05$; Table 5)

Table 2. Correlation coefficient (R^2) for the relationship between *P. juniperinum* fruit characteristics and year, severity of infestation, as well as year*severity combination. Significance levels: *: $P \leq 0.05$; **: $P \leq 0.01$; ***: $P < 0.001$; ns: nonsignificant.

Fruit trait	Year	Parasite severity	Year*severity
Production	0.54 ns	0.46 ns	0.99 ***
% water content	0.36 ns	0.63 ns	0.98 ***
Diameter	0.64 ns	0.24 ns	0.88 *
Thickness	0.17 ns	0.71 *	0.88 *
Dry mass	0.02 ns	0.86 **	0.87 *
Seed length	0.72 *	0.21 ns	0.93 **
Seed dry mass	0.49 ns	0.46 ns	0.95 **

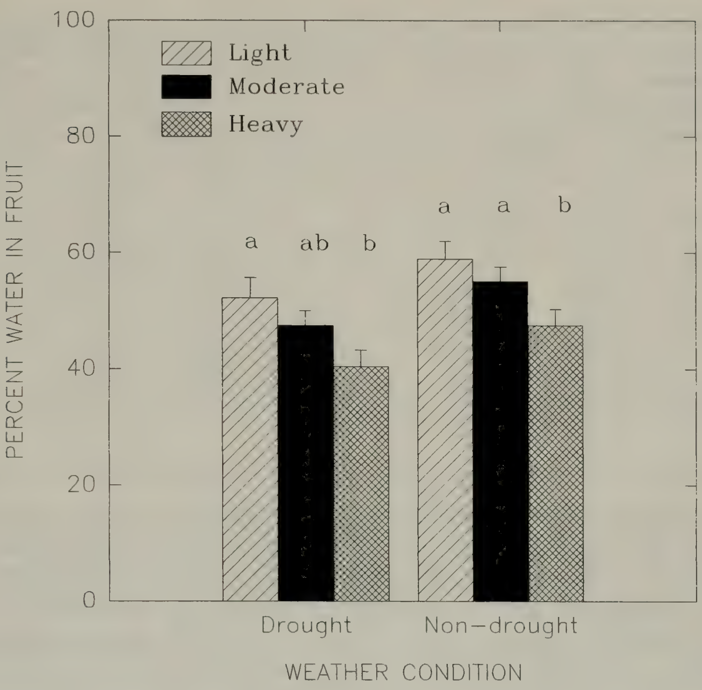


Fig. 4. Fruit water content (Mean ± SE, n = 100 per treatment) of *P. juniperinum* growing on *J. osteosperma* hosts with three levels of infections in Pine creek of southern Nevada. Narrow vertical bars denote standard errors of the means. Within the same weather condition, columns labeled with different letters are significantly different at $P \leq 0.05$.

correlated with year. However, all fruit traits other than seed dry mass were significantly ($P \leq 0.05$; Table 4) correlated with parasite severity.

Discussion

Fruit characteristics of *P. juniperinum* on hosts with three levels of infestation, as well as of uninfested *J. osteosperma* hosts and hosts with three levels of *P. juniperinum* infestation were compared during drought and non-drought periods. The interactive effects of severe drought and heavy parasitism significantly reduced the fruit production and other fruit traits of both hosts and parasites in Pine Creek of the Red Rock National Conservation Area in southern Nevada.

Table 3. Fruit characteristics of *P. juniperinum* growing on *J. osteosperma* hosts with three levels of *P. juniperinum* infections in Pine Creek of southern Nevada (n = 100 per fruit or seed characteristic).

Weather condition	Infection status	Diameter (mm)	Thickness (mm)	Dry mass (mg)	Seed length (mm)	Seed dry mass (mg)
Drought	Light	4.4	3.6	24.7	3.4	11.4
	Moderate	4.4	3.5	23.4	3.3	10.2
	Heavy	4.2	3.3	22.6	3.1	10.0
Non-drought	Light	4.6	3.7	25.9	3.6	12.4
	Moderate	4.5	3.5	23.2	3.6	11.5
	Heavy	4.5	3.5	22.5	3.5	11.1

Table 4. Two-way ANOVA results of the effects of year, severity of infestation, and their interactions on various fruit characteristics of *J. osteosperma.* df = 1 for year; df = 3 for parasite severity and for year*parasite severity combination. Significance levels: *: $P \leq 0.05$; **: $P \leq 0.01$; ***: $P \leq 0.001$; ns: non-significant.

	Year		Parasite severity		Year*severity	
Fruit trait	F	P	F	P	F	P
Production	132.54	0.0014**	48.70	0.0048**	255.16	0.0000***
% water content	100.72	0.0016**	570.05	0.0001***	67.38	0.0002***
Diameter	12.00	0.0742ns	2.33	0.300ns	11.42	0.0395*
Thickness	3.00	0.2254ns	6.33	0.1364ns	10.73	0.0429*
Dry mass	0.44	0.5743ns	13.25	0.0702ns	10.21	0.0458*
Seed length	27.00	0.0351*	4.33	0.1875ns	19.69	0.0188*
Seed dry mass	165.14	0.0060**	86.14	0.0115*	26.67	0.0123*

Weather extremes are an important environmental factor that may lower the reproductive success, particularly the fruit characteristics of *P. juniperium* and its *J. osteosperma* host trees. Insufficient precipitation and considerably above average air temperatures over a period of six months in 1997 may have been an example of such an extreme. The well below average seasonal precipitation and above average air temperatures from January to mid-July 1997 period likely resulted in low soil water content and high soil temperatures. Such severe drought conditions would result in substantial host and parasitic plant water stress. This severe drought was followed by above average monsoonal rainfalls in July and September (NOAA, Red Rock Canyon).

Parasites that heavily infested their hosts also experienced a significant reduction in fruit production and other fruit traits relative to parasites that lightly infested their hosts. In this study, *J. osteosperma* trees were susceptible to *P. juniperinum* in the sense that establishment occurred over time. Significant relationships between parasite severity and fruit characteristics are probably the normal pattern as a consequence of parasitism, regardless of drought. The reduction in fruit production and other fruit characteristics would occur long before the extreme drought in 1997. In general, these relationships between the severity of infestation and fruit characteristics became more prominent under drought stress. No comparative fruit characteristic data are available since the responses of *P.*

Table 5. Correlation coefficient (R^2) for the relationship between *J. osteosperma* fruit characteristics and year, severity of infestation, as well as year*severity combination. Significance levels: *: $P \leq 0.05$; **: $P < 0.01$; ***: $P < 0.001$; ns: non-significant.

Fruit trait	Year	Parasite severity	Year*severity
Production	0.47 ns	0.52 *	0.98 ***
% water content	0.37 ns	0.60 *	0.96 ***
Diameter	0.37 ns	0.62 *	0.99 ***
Thickness	0.15 ns	0.74 **	0.89 **
Dry mass	0.35 ns	0.50 *	0.85 **
Seed length	0.12 ns	0.62 *	0.74 *
Seed dry mass	0.69 *	0.27 ns	0.97 ***

Table 6. Fruit characteristics of uninfected *J. osteosperma* hosts (control) and hosts with three levels of *P. juniperinum* infections in Pine Creek of southern Nevada (n = 100 per fruit or seed characteristic).

Weather condition	Infection status	Diameter (mm)	Thickness (mm)	Dry mass (g)	Seed length (mm)	Seed dry mass (g)
Drought	Control	9.2	7.3	2.4	7.9	1.1
	Light	8.8	7.2	2.4	7.7	1.0
	Moderate	8.4	7.2	2.2	7.3	0.9
	Heavy	8.1	7.0	2.1	6.0	0.9
Non-drought	Control	9.7	7.4	2.6	8.3	1.3
	Light	9.3	7.4	2.5	8.1	1.3
	Moderate	9.0	7.2	2.3	7.6	1.2
	Heavy	8.8	7.1	2.4	7.4	1.1

juniperinum and its *J. osteosperma* hosts to drought were not previously investigated.

Phoradendron juniperinum are autotrophic hemiparasites (Kuijt 1969; Calder and Bernhardt 1983; Lei 1999), but must acquire water and mineral nutrients from its *J. osteosperma* host plant through direct xylem connections (Ehleringer et al. 1986). In general, *Phoradendron* species compete aggressively with their hosts for water and nutrients (Calder and Bernhardt 1983). A combination of severe drought and heavy *P. juniperinum* infestation would impose a substantial

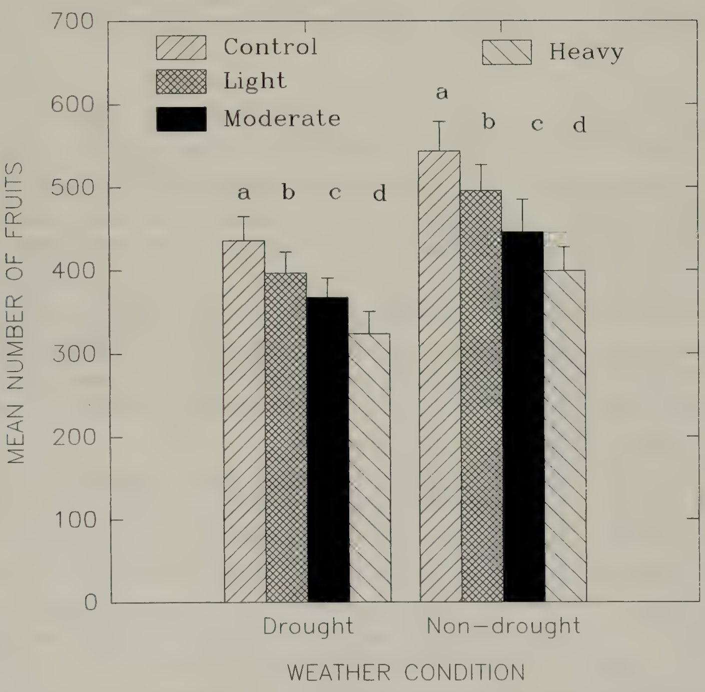


Fig. 5. Fruit production (Mean ± SE, n = 85) of uninfested *J. osteosperma* hosts (control) and hosts with three levels of *P. juniperinum* infections in Pine creek of southern Nevada. Narrow vertical bars denote standard errors of the means. Within the same weather condition, columns labeled with different letters are significantly different at $P \leq 0.05$.

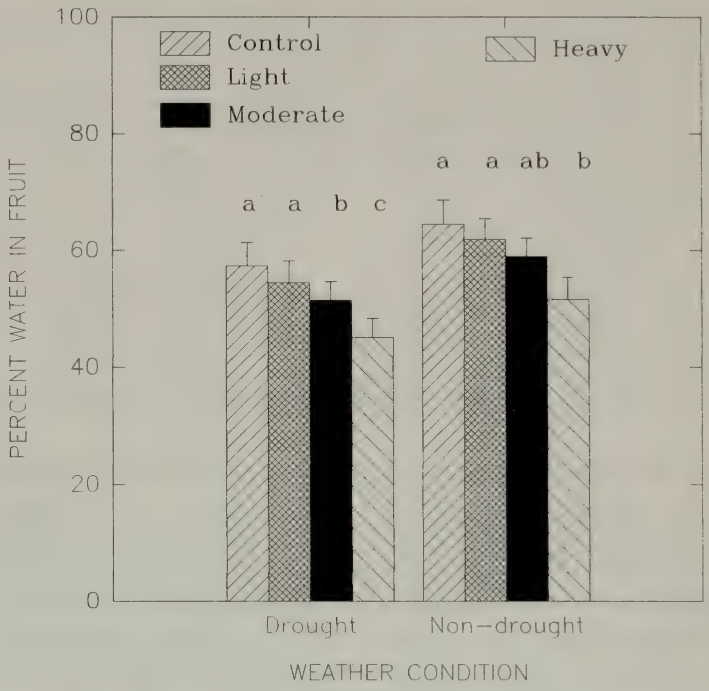


Fig. 6. Fruit water content (Mean ± SE, n = 85) of uninfested *J. osteosperma* hosts (control) and hosts with three levels of *P. juniperinum* infections in Pine creek of southern Nevada. Narrow vertical bars denote standard errors of the means. Within the same weather condition, columns labeled with different letters are significantly different at $P \leq 0.05$.

physiological stress on its *J. osteosperma* hosts. Within a single, heavily-infested host under normal (non-drought) conditions, parasites experience intraspecific interactions, especially density-dependent exploitation and interference competition (Smith 1996). In this study, some *P. juniperinum* individuals had a significantly lower fruit production than others. Occasional severe or prolonged droughts are likely to increase the intensity of intraspecific competition. Consequently, the overall reproductive success, including fruit characteristics, of *P. juniperinum* would be constrained by resource and space within the host. In this study, drought appeared to have a more detrimental effect on *P. juniperinum* than on its hosts because some established *P. juniperinum* individuals on heavily parasitized trees exhibited a substantially lower fruit production.

Uninfested or lightly infested *J. osteosperma* trees appeared to be tolerant to water and heat (drought) stress, and were capable of abundant fruit production in periodically stressful desert environment. Nevertheless, *J. osteosperma* hosts with severe infestation are likely to experience a limited reproductive success during periods of drought. *Juniperus osteosperma* trees are already under considerable infestation stress, and the additional stress of drought weakens host trees enough to limit their reproductive success. Drought stress accentuates or accelerates the detrimental effects of *P. juniperinum* infestation. *Juniperus osteosperma* trees with severe infestation would gradually decline in fruit characteristics compared to similar trees with no infestation. This decline would occur over many years, if not several decades. Aridity is a permanent feature in the warm Mojave Desert of southern Nevada. Drought, however, is a temporary feature, occurring when precipitation falls below normal. Results of this study suggest that combined effects of heavy parasitism and occasional severe droughts can significantly limit certain aspects of reproductive success, particularly fruit characteristics, of both parasitic *P. juniperinum* and its *J. osteosperma* host plants.

Acknowledgments

Sincere appreciation is expressed to Steven Lei, David Valenzuela, and Shevaun Valenzuela for providing valuable field and laboratory assistance. Appreciation is also expressed to the Department of Biology of the Community College of Southern Nevada (CCSN) for providing logistical support.

Literature Cited

Analytical Software 1994. Statistix 4.1, an interactive statistical program for microcomputers. Analytical Software, Tallahassee, Florida.

Calder, M. and P. Bernhardt. 1983. The biology of mistletoes. Academic Press, New York.

Dawson, T. E., J. R. Ehleringer, and J. D. Marshall. 1990. Sex-ratio and reproductive variation in the mistletoe *Phoradendron juniperinum* (Viscaceae). Amer. J. Botany 77:585–589.

Ehleringer, J. R., C. S. Cook, and L. L. Tieszen. 1986. Comparative water use and nitrogen relationships in a mistletoe and its host. Oecologia 68:279–284.

Glatzel, G. 1983. Mineral nutrition and water relations of hemiparasitic mistletoes: a question of partitioning experiments with *Loranthus europaeus* on *Quercus petraea* and *Q. robur.* Oecologia 56:193–201.

Hollinger, D. Y. 1983. Photosynthesis and water relations of the mistletoe, *Phoradendron villosum,* and its host, the California valley oak, *Quercus lobata.* Oecologia 60:396–400.

Kuijt, J. 1969. The biology of parasitic flowering plants. University of California Press, Berkeley, California.

Lei, S. A. 1999. Host-parasite relationship between Utah juniper and juniper mistletoe in the Spring Mountains of southern Nevada. Pages 99-104 in Proceedings: Ecology and management of pinyon-juniper communities within the interior west. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah.

Munz, P. A. 1974. A flora of Southern California. University of California Press, Berkeley, California.

National Oceanic and Atmospheric Administration (NOAA). 1998. Local climatological data: annual summary with comparable data, Las Vegas, Nevada. National Climatic Data Center, Ashville, North Carolina.

Schulze, E. D. and J. R. Ehleringer. 1984. The effect of nitrogen supply and water-use efficiency of xylem-tapping mistletoes. Planta 162:268–275.

Schulze, E. D., N. C. Turner, and G. Glatzel. 1984. Carbon, water and nutrient relations of two mistletoes and their hosts: a hypothesis. Plant, Cell and Environment 7:293–299.

Smith, R. L. 1996. Ecology and Field Biology (5th ed.). Harper Collins College Publishers, Inc., New York.

Accepted for publication 19 June 2000.

Bull. Southern California Acad. Sci.
100(2), 2001, pp. 96–99

Spatial Distribution of Blackbrush (*Coleogyne ramosissima* Torr.) Populations in the Mojave Desert

Simon A. Lei

Department of Biology, WDB, Community College of Southern Nevada,
6375 West Charleston Boulevard, Las Vegas, Nevada 89146-1139

The pattern of spatial distribution of a plant population is a fundamental characteristic of that population, but it is a feature that is extremely difficult to describe in precise and meaningful terms (Clark and Evans 1954). At the local level, even in a relatively homogeneous environment, individuals in a single plant population can be distributed randomly, clumped together, or in highly regular patterns (Cunningham and Saigo 1999).

Blackbrush (*Coleogyne ramosissima* Torr.) shrubs are established primarily along the Colorado River drainage and several adjacent enclosed basins of the Great Basin-Mojave Desert transition (Bowns and West 1976). *Coleogyne ramosissima* shrubs are a common vegetation type in mid-elevations of the Mojave Desert, with creosote bush-white bursage (*Larrea tridentata-Ambrosia dumosa*) shrublands occurring on valley floors and lower desert mountain slopes and with pinyon pine-Utah juniper (*Pinus monophylla-Juniperus osteosperma*) woodlands occurring at higher mountain slopes (Lei 1995).

Some ecological aspects of *C. ramosissima* and its shrublands have been documented (Beatley 1974 and 1976; Bowns 1973; Bowns and West 1976; Bradley 1964; Brown 1982; Callison and Brotherson 1985; Korthuis 1988; Lei 1995, 1999a, b; Lei and Walker 1995, 1997a, b; and Pendleton et al. 1995 and 1999). However, *C. ramosissima* was selected as a representative species for such a study because the spatial distribution of individuals and populations within the *C. ramosissima* shrublands in isolated mountain ranges in the Mojave Desert has not been quantatively investigated. From casual observations, the spatial distribution of *C. ramosissima* individuals and populations appears to be clumped throughout the Mojave Desert. This hypothesis was tested by field measurements with appropriate statistical analysis.

Field studies were conducted at fully developed *C. ramosissima* shrublands throughout the Mojave Desert during July 2000. The five study sites were located in the Spring and Newberry Mountains of southern Nevada, the Clark Mountain of southeastern California, the Virgin Mountains of northwestern Arizona, and the Mormon Range of southwestern Utah (Table 1). Elevation varied considerably, ranging from 1,250 m in the Mormon Range to 1,450 m in the Spring Mountains. These five sites were fairly representative of *C. ramosissima* populations, and formed nearly monospecific blackbrush vegetation zones in the Mojave Desert. Each of the five sites represented an isolated mountain range for *C. ramosissima* population.

The weather pattern of the Mojave Desert is characterized by wide-ranging daily air temperatures, high year-round air temperatures, extremely high potential evaporation, little cloud cover, low relatively humidity, low annual precipitation

Table 1. Geographical characteristics of the five *C. ramosissima* study sites. Location, as well as approximate latitude (N), longitude (W), and elevation (m) are shown. Mountain ranges are arranged alphabetically in the Mojave Desert.

Location	County, State	Latitude	Longitude	Elevation
Clark Mountain	San Bernadinom, CA	35°05′	115°50′	1300
Mormon Range	Washington, UT	37°20′	114°00′	1250
Newberry Mountains	Clark, NV	35°20′	114°50′	1300
Spring Mountains	Clark, NV	35°50′	115°35′	1450
Virgin Mountains	Mohave, AZ	36°50′	114°00′	1300

(Lei 1999b). The Mojave Desert resembles the Mediterranean-type climate characterized by hot, dry summers and cool, wet winters. Episodic monsoonal winds and thunderstorms occur during summer seasons. Winter rainfalls, although varying considerably from year to year, contribute to most of the total annual precipitation (Lei 1999b). The terrain consists of rocky slopes and alluvial fans dissected by dry wash channels. Soil profiles are poorly developed, and soils are composed primarily of weathered granite and limestone bedrock. Organic decomposition and soil formation are slow due to the arid nature of the region (Lei 1999b).

Within each site, the spatial distribution of *C. ramosissima* population was examined on a 10-ha plot. The nearest neighbor method was used to determine whether shrubs of the same species are distributed at random, are clumped, or are regular (Barbour et al. 1987). At each site, 100 random points were distributed evenly among the four parallel transects located on the 10-ha plot. Intervals between two parallel transects are 20 m apart. However, intervals between two points within a transect were randomly selected to avoid biased field measurements. The distance measured was from the center of individual *C. ramosissima* located closest to the random point to the center of its nearest *C. ramosissima* neighbor.

One-way Analysis of Variance (ANOVA), followed by Tukey's Multiple Comparison Test (Analytical Software 1994) was used to detect differences among distances between one *C. ramosissima* to its nearest *C. ramosissima* neighbor, and to compare site means when a significant distance effect was detected, respectively. Mean distance values were presented with standard errors, and statistical significance was determined at $P \leq 0.05$.

The ratio of the observed mean distance to the expected mean distance (R-value) served as a measure of departure from randomness (Clark and Evans 1954). The nearest neighbor method (Clark and Evans 1954) was used to determine whether the *C. ramosissima* populations were randomly distributed within the *C. ramosissima* shrublands. The significant difference in the value of R for *C. ramosissima* populations was tested with the c value of 1.96, representing the 5 % level of significance for a two-tailed test (Clark and Evans 1954; McClave and Dietrich 1991).

Mean distances between *C. ramosissima* and its nearest *C. ramosissima* neighbor were significantly different ($P \leq 0.05$; Table 2) among the five isolated mountain ranges in the Mojave Desert. The mean distances ranged from 210 cm in the Mormon Range in southwestern Utah to 275 cm in the Clark Mountains of southeastern California.

Coleogyne ramosissima populations among the five isolated mountains ranges were strongly aggregated, ranging from 0.13 in the Mormon Range to 0.17 in the

Table 2. Distance (mean ± SE) and R-values from one individual *C. ramosissima* to its nearest *C. ramosissima* neighbor in five isolated mountain ranges of the Mojave Desert (N = 100 per mountain range). Mean values followed by different letters indicate significant differences at $P \leq 0.05$ using Tukey's Multiple Comparison Test.

Location	Mean distance (cm)	R-value
Clark Mountain	275 ± 24.7 a	0.17
Mormon Range	210 ± 19.4 b	0.13
Newberry Mountains	251 ± 22.3 ab	0.16
Spring Mountains	239 ± 28.4 ab	0.15
Virgin Mountains	247 ± 11.2 ab	0.16

Clark Mountains (Table 2). When examining the spatial distribution of *C. ramosissima* populations, there was a tightly clustering of mean values of distance from one *C. ramosissima* plant to another and for R-values. For the spatial distribution in this study, $R \ll 1.0$, indicating a significant departure from random expectation in the direction of aggregated spacing by the c test. According to the distance to nearest neighbor as a measure of spatial distribution in plant populations, $R = 0$ in a maximum aggregation, since all of the individuals occupy the same locus and the distance to nearest neighbor is therefore 0. In contrast, $R = 2.1491$ in a maximum uniformity, since individuals will be distributed as evenly and widely as possible in a hexagonal pattern (Clark and Evans 1954). The ratio of observed to expected mean distance to nearest neighbor provides a measure of the degree to which the distributional pattern of the observed population deviates from random expectation (Clark and Evans 1954).

The distance from one individual plant to another provides a variable for the measurement of spacing that obviates the use of quadrats, and, therefore, eliminates the effect of quadrat size (Goodall 1953). The measure of spacing in this study is a measure of the degree to which the distribution of individuals in *C. ramosissima* populations at given areas departs from that of a random distribution. Thus, randomness is a spatial concept, intimately dependent upon the boundaries of the space chosen by the investigator (Clark and Evans 1954). In this study, all five *C. ramosissima* populations on isolated mountains ranges clearly departed from random expectation with a high degree of significance as the distance to nearest neighbor is concerned. Although significant differences in mean distances were detected, only a slight difference in the degree of aggregation was found among the five *C. ramosissima* populations in the Mojave Desert.

Acknowledgments

I gratefully acknowledge Steven Lei, David Valenzuela, and Shevaun Valenzuela for valuable field assistance. Steven Lei assisted with statistical analysis and provided helpful comments on earlier versions of this manuscript.

Literature Cited

Analytical Software. 1994. Statistix 4.1, an interactive statistical program for microcomputers. Analytical Software, St Paul, Minnesota.

Barbour, M. G., J. H. Burk, and W. D. Pitts. 1987. Terrestrial plant ecology, Second Edition. The Benjamin/Cummings Publishing Company, Inc., Menlo Park, California.

Beatley, J. 1974. Effects of rainfall and temperature on the distribution and behavior of *Larrea divaricata* (creosote-bush) in the Mojave Desert of Nevada. Ecology 55:245–261.

Beatley, J. 1976. Vascular plants of the Nevada Test Site and Central-southern Nevada: ecologcial and geographical distributions. National Technical Information Service, United States Department of Commerce, Springfield, Virginia.

Bowns, J. 1973. An autecological study of blackbrush (*Coleogyne ramosissima* Torr.) in southern Utah. Unpublished dissertation, Utah State University, Logan, Utah.

Bowns, J. and N. West. 1976. Blackbrush (*Coleogyne ramosissima* Torr.) on southern Utah rangelands. Department of Range Science, Utah State University. Utah Agricultural Experiment Station, Research Report 27.

Bradley, W. G. 1964. The Vegetation of the Desert Game Range with special reference to the desert bighorn. Trans. Desert Bighorn Council 8:43–67.

Brown, D. 1982. Biotic communities of the American Southwest: United States and Mexico. The University of Arizona for the Boyce Thompson Southwestern Arboretum, Tucson, Arizona.

Callison, J. and J. Brotherson. 1985. Habitat relationship of the blackbrush community (*Coleogyne ramosissima*) of southern Utah. The Great Basin Naturalist 45:321–326.

Clark, P. J. and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:155–162.

Cunningham, W. P. and B. W. Saigo. 1999. Environmental Science, Fifth edition. WCB McGraw-Hill, Boston, Massachusettes.

Goodall, D. W. 1953. Objective methods for the classification of vegetation. I. The use of positive interspecific correlation. Australian Journal of Botany 1:39–63.

Korthuis, S. 1988. *Coleogyne ramosissima.* In: Fischer, William C., Compiler. The Fire Effects Information System (Data base). Missoula, Montana: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Intermountain Fire Sciences Laboratory. Magnetic tape reels; 9 track; 1600 bpi, ASCII with common LISP present.

Lei, S. A. 1995. A gradient analysis of blackbrush (*Coleogyne ramosissima* Torr.) communities in southern Nevada. Unpublished thesis. University of Nevada, Las Vegas, Nevada.

Lei, S. A. and L. R. Walker 1995. Composition and distribution of blackbrush (*Coleogyne ramosissima*) Torr. communities in southern Nevada. p. 191–195, *in* E. D. McArthur, J. S. Haley, and D. K. Mann, compilers. Proceedings: wildland shrub and arid land restoration symposium, General Technical Report INT-GTR-315, Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Lei, S. A. and L. R. Walker 1997a. Classification and ordination of *Coleogyne* communities in southern Nevada. The Great Basin Naturalist 57:155–162.

Lei, S. A. and L. R. Walker 1997b. Biotic and abiotic factors influence the distribution of *Coleogyne* communities in southern Nevada. The Great Basin Naturalist 57:163–171.

Lei, S. A. 1999a. Phenological events and litterfall dynamics of blackbrush in southern Nevada. p. 113–118 *in* E. D. McArthur, W. K. Ostler, and C. L. Wambolt, compilers. Proceedings: Shrubland Ecotones, Proceedings RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Lei, S. A. 1999b. Ecological anatomy of seven xerophytic shrub species in southern Nevada. p. 206–211 *in* E. D. McArthur, W. K. Ostler, and C. L. Wambolt, compilers. Proceedings: Shrubland Ecotones, Proceedings RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

McClave, J. T. and F. H. Dietrich. 1991. Statistics, Fifth Edition. Dellen Publishing company, San Francisco, California.

Pendleton, B. K., S. E. Meyer, and R. L. Pendleton. 1995. Blackbrush biology: insights after three years of a long-term study. p. 223–227, *in* E. D. McArthur, J. S. Haley, and D. K. Mann, compilers. Proceedings: wildland shrub and arid land restoration symposium, General Technical Report INT-GTR-315, Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Pendleton, R. L., B. K. Pendlton, and S. D. Warren. 1999. Response of blackbrush seedlings to inoculation with arbuscular mycorrhizal fungi. p. 245–251 *in* E. D. McArthur, W. K. Ostler, and C. L. Wambolt, compilers. Proceedings: Shrubland Ecotones, Proceedings RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Accepted for publication 28 January 2001.

Bull. Southern California Acad. Sci.
100(2), 2001, pp. 100–108

Postfire Seed Bank and Soil Conditions in a Blackbrush (*Coleogyne ramosissima* Torr.) Shrubland

Simon A. Lei

Department of Biology, Community College of Southern Nevada,
6375 West Charleston Boulevard, WDB, Las Vegas, NV 89146-1139

Abstract.—Ten-year postfire seed bank and soil conditions were quantitatively investigated in a blackbrush (*Coleogyne ramosissima*) shrubland in Sandy Valley of southern Nevada. A severe, lightning-induced fire occurred in June 1987, creating a nearly barren landscape. Seed density of woody species at the soil surface and in the top 3 cm of soil was significantly lower in burned areas compared to adjacent unburned areas. However, within the burned areas, no significant differences were detected in seed density of woody species. Although seed transport from adjacent unburned areas out onto the burns was minimal, evidence of limited long-distance dispersal of *C. ramosissima* seeds was found. Soil moisture and organic matter decreased significantly, whereas soil pH, soil temperature, bulk density, and compaction increased significantly in burned areas compared to unburned areas. Nevertheless, soil salinity did not differ significantly after burning. Limited long-distance dispersal, extremely low soil seed densities, as well as adverse weather and impoverished edaphic conditions were some of the primary obstacles to reestablishment of *C. ramosissima* plants and their shrublands.

Fire and its impact on soil seed bank and soil conditions have been of interest to many ecologists, especially in major shrublands of the desert Southwest. Fires occur frequently at elevations above 1,650 m in the Mojave Desert woodlands because the cool, semiarid climate results in a substantial accumulation of fuel (Humphrey 1974). However, fires are less frequent at mid- and lower elevations (below 1,650 m) of the Mojave Desert shrublands primarily due to limited biomass and vegetation cover, wide spacing between shrubs, and insufficient accumulation of flammable material (Brown and Minnich 1986). Blackbrush (*Coleogyne ramosissima*) shrublands are located at mid-elevations. Shrub species in *C. ramosissima* communities have a low recovery rate years after fire, and are subject to long-standing changes in the structure and species composition in southeastern California (Minnich 1995) and southern Nevada (Lei 2000). Fire greatly reduces woody vegetation over an extensive area, thus exacerbating re-establishment by requiring long-range seed dispersal from widely scattered unburned individuals that provide local seed sources (Minnich 1995).

Coleogyne ramosissima produce seeds that usually fall near the parent plants (Lei, personal observations). *Coleogyne ramosissima* plants are capable of long-range seed dispersal by wind, water (downslope movement), or fauna (Brown and Minnich 1986; Minnich 1995). Evidence of long-range wind, water, or fauna dispersal from adjacent unburned areas to burned areas was found since a few seeds were observed on the surface near the center of large burned areas in southern Nevada (Lei, personal observations).

A seed bank is an aggregation of ungerminated seeds potentially capable of replacing adult plants through time (Leck et al. 1989). The potential for replacing adult plants is essential. If seeds get permanently buried too deeply, they can be considered lost from the desert seed bank, as they would not be involved in germination, granivory, redistribution or other processes that directly relate to seed bank dynamics (Leck et al. 1989). Seeds of desert shrubs generally cannot emerge from below 4 cm (Leck et al. 1989). However, seeds in desert soils are distributed mostly near the surface; approximately 80 to 90 % of seeds are found in the upper 2 cm of soil (Reichman 1975). *Coleogyne ramosissima* vegetation zones do not form long-term or permanent desert seed banks, and reestablishment of *C. ramosissima* may also depend on rodents transporting seed from the adjacent unburned areas out onto the burns, a small possibility for large disturbances (Pendleton et al. 1995). *Coleogyne ramosissima* seeds are buried by rodents to a few centimeters in depth; these seeds may germinate from rodent caches after abandonment (Bowns 1973; Bowns and West 1976).

Following a severe fire, soil organic matter and percent pore space decrease significantly. On the contrary, fire significantly increases soil pH, temperature, compaction, and bulk density in *C. ramosissima* shrublands of southern Nevada (Lei 2000).

Fire has been responsible for altering and severely damaging *C. ramosissima* vegetation zones in southern Nevada (Lei 2000). *Coleogyne ramosissima* stands do not recover from fire disturbance, and much acreage of this vegetation type is being lost due to an increase in fire frequency (Lei 2000). The time required for a complete postfire recovery of vegetation is still unknown in *C. ramosissima* shrublands in southern Nevada and throughout its range. Postfire woody vegetation recovery in the *C. ramosissima* shrublands has been documented (Beatley 1974, 1975 and 1980; Callison et al. 1985; Korthuis 1988; Lei 2000; and Minnich 1995). However, the possible effects of fire on seed density of woody plants remain poorly understood. The objectives of this article were to quantitatively evaluate soil parameters, along with the presence and seed density of woody species ten years after burning in Sandy Valley of southern Nevada.

Materials and Methods

Study Site

The study was conducted during summer 1998 in Sandy Valley, along State Highway 160, located on the lower west-facing slopes of the Spring Mountains (approximately 36°00′N, 115°40′W; 1,350 to 1,400 m in elevation) in southern Nevada. *Coleogyne ramosissima* forms a nearly monospecific vegetation zone at mid-elevations, with only a scattered distribution of other shrub species (Lei and Walker 1997; Lei 2000).

Burned and unburned areas were once similar in species composition, vegetation cover, community structure, soil, geology, and geomorphic surfaces (Tim Rash, Personal Communication). Burned and unburned areas were separated by a two-lane highway, forming two distinct landscapes. The fire was started in June 1987 by lightning from a summer monsoonal thunderstorm, and burned approximately 4,000 ha from the upper *C. ramosissima* elevational boundary through the upper portions of the creosote bush-white bursage (*Larrea tridentata-Ambro-*

sia dumosa) zone. This extensive fire provided an opportunity to examine postfire seed density of woody species, as well as edaphic characteristics of a *C. ramosissima* shrubland.

Fire History

Sandy Valley is under the jurisdiction of the Las Vegas District of the Bureau of Land Management (BLM). Fire data were obtained from fire reports and atlases of the BLM, which provided the most reliable source of *C. ramosissima* fire history available in Sandy Valley. Topographic maps and aerial photographs were used to determine fire boundaries and to map the extent of burns. The burn margins and scars in the *C. ramosissima* vegetation zone were often visible and identifiable based on the presence or absence of the dominant plant species.

Seed and Soil Collections

Seeds of woody species and their corresponding soil samples were collected from five, 1 m^2 plots randomly situated along each of 20, 150 m transects situated in both burned and unburned areas. Transects were oriented parallel to, and at least 50 m from, the edge of the road. In burned areas, 75 plots were located at the burn-edge (8 m from the edge of the burn scar), one-quarter of the distance to the burn-center (300 m from the burn-edge), and in the center of the burn (600 m from the burn-edge). In unburned areas, five transects were located 100 m from the burn-edge.

Soils were sampled from the entire 1 m^2 plots to a depth of 3 cm. After removal of surface rocks and litter, soils were collected from both inter-plant gaps and directly under existing plant canopies in order to measure the full range of the seed bank and heterogeneity of soil characteristics. Soils collected from open spaces and under plant canopies were then pooled per plot after thorough mixing. Seeds on ground surface were observed using a magnifying glass. Each soil sample was sifted through a 1-mm sieve to search for seeds. Numbers of seeds of woody species were individually counted in the field. Density was expressed as number of seeds per 1 m^2. Sieved and oven-dried soils were retained for laboratory analyses at the Community College of Southern Nevada (CCSN).

Soil Analyses and Measurements

In the field, soil temperatures at the surface and at a depth of 3-cm were recorded with a soil thermometer located at the central point within each of the 100 plots. Soil temperatures were recorded from mid-morning hours to minimize diurnal soil temperature variation due to sun angle. Soil temperatures were recorded simultaneously with soil moisture and sample collection to ensure comparability. Soil compaction was estimated using a penetrometer that was inserted into the soil after removing stony surface pavements. Percent pore space was determined using the following equation: Pore space $= 100 - (D_b/D_p \cdot 100)$, where D_b is the bulk density of the soil and D_p is the average particle density, usually about 2.65 g/cc (Hausenbuiller 1972; Davidson and Fox 1974).

In the laboratory, the fresh soil samples were weighed, dried in a 65°C oven until they reached a constant mass, and reweighed to determine gravimetric water content. Soil bulk density was assessed by dividing dry mass by volume. Soil pH was determined on a saturation paste acquired by mixing equal volumes of dry

Table 1. Mean seed density of wood plants (no./m^2; N = 100 plots) at the ground surface in burned and adjacent unburned areas of the *C. ramosissima* vegetation zone in Sandy Valley. Within burned areas, seed density is shown at three distances from the fire-edge. Mean values in rows followed by different letters are significantly different at $P \leq 0.05$.

		Burned area		
Plant species	Unburned area	8 m	300 m	600 m
Coleogyne ramosissima	0.14 a	0.07 b	0.06 b	0.04 b
Encelia virginensis	0.17 a	0.09 b	0.07 b	0.07 b
Gutierrezia sarothrae	0.24 a	0.13 b	0.12 b	0.11 b
Lycium andersonii	0.04 a	0 b	0 b	0 b
Menodora spinescens	0.05 a	0 b	0 b	0 b
Thamnosma montana	0.07 a	0 b	0 b	0 b
Yucca brevifolia	0.04 a	0 b	0 b	0 b

soil saturated with deionized water (McLean 1982). Total organic matter was obtained for samples that were pre-dried at 65°C for 72 h, followed by mass loss on ignition at 550°C for 4 h (Black 1965). Soil salinity (total soluble salts) was acquired by an electrical conductivity bridge, using a slurry consisting of equal parts of soil to distilled water paste (Rhoades 1982).

Statistical Analyses

One-way analysis of variance (ANOVA; Analytical Software 1994) was used to compare means of seed densities, as well as to compare corresponding soil attributes between burned and unburned areas in the *C. ramosissima* vegetation zone. ANOVA was also used to detect differences among burned areas only. Burned areas were subdivided into three distances from the fire edge. Tukey's multiple comparison test (Analytical Software 1994) was then performed to compare means when a significant fire effect was detected between burned and unburned areas, as well as among burned areas only. Student t-tests (Analytical Software 1994) were conducted to compare soil temperatures between the soil surface and at 3-cm depth in burned and unburned areas. Mean values are presented with standard errors, and P-values less than or equal to (≤) 0.05 are reported as statistically significant.

Results and Discussion

Seed Densities

For all woody species evaluated, soil seed density was significantly lower ($p \leq 0.05$; Tables 1 and 2) in burned compared to unburned areas in Sandy Valley of southern Nevada. Specifically, *Gutierrezia sarothrae* density was highest in both treatments at both soil surface and 3 cm depths (0.14 and 0.10 seeds/m^2, respectively), followed by *Encelia virginensis* density at the surface (0.17 seeds/m^2 in unburned and 0.08/m^2 in burned areas) and *Coleogyne ramosissima* at 3 cm depths (0.10/m^2 in unburned and 0.02/m^2 burned areas).

Within burned or unburned areas, seed density of *C. ramosissima, E. virginensis, G. sarothrae, Lycium andersonii,* and *Menodora spinescens* was significantly higher ($P \leq 0.01$) on the surface of soil (Table 1) than under 3 cm of soil (Table 2). A number of seeds were found deeper than 3 cm below the soil surface in

Table 2. Mean seed density of woody plants (no./m^2; N = 100 plots) at the top 3 cm of soil in burned and adjacent unburned areas of the *C. ramosissima* vegetation zone in Sandy Valley. Within burned areas, seed density is shown at three distances from the fire-edge. Mean values in rows followed by different letters are significantly different at $P \leq 0.05$.

Plant species	Unburned area	Burned area		
		8 m	300 m	600 m
Coleogyne ramosissima	0.10 a	0.03 b	0.02 b	0.02 b
Encelia virginensis	0.09 a	0.04 b	0.04 b	0.03 b
Gutierrezia sarothrae	0.17 a	0.07 b	0.05 b	0.05 b
Lycium andersonii	0	0	0	0
Menodora spinescens	0	0	0	0
Thamnosma montana	0.05 a	0 b	0 b	0 b
Yucca brevifolia	0	0	0	0

unburned areas (Lei, personal observation), presumably due to animals (rodents) placing them in caches and, to a lesser extent, wind-blown sand burying seeds several centimers beneath the soil under shrub canopies through time.

No significant differences were found at various distances within burned areas in this study. In addition to long-distance seed dispersal, scattered surviving individuals of woody plants on unburned "fire islands" throughout the burns would provide local seed source through time (Minnich 1995). Nevertheless, no such "fire islands" existed in this study because all woody plants were eradicated by fire, and therefore, woody seeds found on the surface in burned areas depended on long-distance dispersal.

Seed banks of the warm deserts are composed primarily of annual species; perennial species do not form persistent seed banks (Leck et al. 1989). Shrubs in warm deserts have a minimal dependence on seed banks for regeneration and protection against climatic uncertainty or other environmental stochascity (Leck et al. 1989). Their strategy is to produce a few seeds almost every year, most of which do not persist in the seed bank (Boyd and Brum 1983). Examination of habitat differences within the *C. ramosissima* shrubland in Sandy Valley indicates that seed bank dynamics are governed by local plant distributions and local flowering and fruiting events. Soil seed densities do not correlate well with plant densities in time or space (Leck et al. 1989). In this study, the significantly fewer number of seeds in burned areas suggests that *C. ramosissima* shrubland will require a long period of time to return to pre-burn conditions following fire disturbance.

Soil Properties

Edaphic factors appeared to be critical for seed germination of *C. ramosissima* and associated woody taxa in Sandy Valley. Soil physical and chemical characteristics were significantly altered ten years after burning. However, no significant differences were detected at various distances within extensive burned areas. With the exception of soil salinity (0.3 in unburned and 0.4 in burned areas; Table 4), all soil parameters measured differed significantly between burned and unburned areas ten years after burning.

Burned areas had significantly higher ($p \leq 0.05$; Table 4) soil temperatures

(39.7 to 40.7°C) at or near the surface than unburned areas (37.5°C). Soil temperatures at the surface and at 3-cm depth were significantly higher in burned than unburned areas in southern Nevada (Lei 2000). Conversely, soil moisture was significantly higher in unburned (1.1 %) than in burned (0.6 to 0.8 %; Table 4) areas. Depending on fuel accumulation rates, burning should be expected to have a long-term effect on soil moisture and soil temperature, at least in the mineral horizon. Surface litter allows for both water retention (reduced evapotranspiration) and cooling (shades the mineral soil also affecting evaporation). Surface litter affects soil moisture and soil temperature long after burning only further emphasizes the long-term effect of fire on *C. ramosissima* vegetation zones.

Soil pH was higher ($P \leq 0.05$; Table 4) in burned than in unburned areas of the *C. ramosissima* vegetation zone. Soil pH increased significantly from 7.7 in unburned to 8.1 in burned areas at the *C. ramosissima* zone (Table 4). Fire tends to increase pH, making soils more basic. The hydrogen ion concentration decreases after incineration, and raising the soil pH is usually significant in the upper 10 cm (Scotter, 1963; Raison 1979; Wright and Bailey 1982).

Percent pore space was significantly lower ($P \leq 0.05$; Table 4) in burned (45.7 to 47.1 %) compared to unburned (50.2 %) areas. Desert soils of southern Nevada are relatively high in sand and gravel. Sandy soils typically have a pore space of 35 to 50 % (Davidson and Fox 1974), which is in agreement with this study. The decrease in percent pore space may also reflect the reduction in soil organic matter (4.1 % without burn; 1.9 to 2.0 % with burn). Organic matter is generally clay-sized, which has a substantially smaller pore space than sand and silt. Organic matter also decreases bulk density of the soil because it is less dense (lighter) than a corresponding volume of mineral soil (Barbour et al. 1987), which is consistent with this study, indicating that soil bulk density increased significantly (Table 4) in burned areas. The carbon content is inversely correlated with the bulk density of the soil (Barbour et al. 1987). In this study, the increase in soil bulk density of burned areas, along with the decrease in pore space, would most likely increase water-holding capacity, particularly at depth. On the soil surface, however, this water may fall within the evaporation zone and, thus, be subject to evaporative losses.

The increase in soil compaction with burning (+0.8 to +1.2 kg/cm^2; Table 4) is also consistent with the increase in bulk density and decrease in pore space. The more compact the soil, the less likely that evaporation will occur. Gravimetric water in small pore spaces is very tightly held against evaporative and plant-uptake losses. Yet, the increase in soil compaction in burned areas may inhibit root growth of woody taxa that are adapted to a looser soil condition (Davidson and Fox, 1974).

Weather Conditions

Southern Nevada experienced several episodes of drought in recent years (Table 3), resulting in widespread plant water stress. Droughts in southern Nevada are unpredictable in terms of their duration and timing. Rainfall variability is a major factor in the occurrence of drought. Most recently, a major drought began in summer 1995, and reached its greatest intensity during the first six months of 1997. According to weather records between 1987 and 1997, only three consec-

Table 3. Mean annual precipitation (mm) and air temperature (C°) from 1988 through 1997. Official postfire weather data (NOAA, Las Vegas) were obtained from the McCarran Airport in Las Vegas, near Sandy Valley. Individual annual precipitation and air temperature values (1988–1997) are compared with the overall mean annual precipitation and air temperature values (1936–1997), respectively. The overall mean annual precipitation is approximately 100 mm, and mean air temperature is 19.2°C.

Year	Precip. (mm)	% diff. from mean	Air temp. (°C)	% diff. from mean
1988	58.2	−52.8	19.9	+3.6
1989	53.6	−60.4	20.4	+6.1
1990	95.3	−4.8	19.7	+2.6
1991	103.1	+3.1	19.5	+3.2
1992	250.9	+86.0	20.1	+4.6
1993	128.3	+24.8	19.7	+2.6
1994	65.0	−42.4	20.6	+7.0
1995	93.7	−6.5	20.6	+7.0
1996	70.1	−35.2	20.7	+7.5
1997	92.2	−8.1	20.3	+5.6

utive years, from 1991 through 1993, revealed above average rainfall in Sandy Valley. Mean annual air temperatures, on the contrary, did not vary considerably, ranging from 0.3 to 1.5 °C only (Table 3). Mean annual precipitation revealed a considerably greater fluctuation than mean annual air temperatures from 1988 through 1997. Although 1991–1993 had above average rainfall, mean annual air temperatures from the 1988–1997 period were consistently higher than mean annual air temperatures from the 1936–1997 period (Table 3).

Rainfall must be adequate during the winter and early spring to trigger seed germination, and during the spring and early summer to support seedling establishment in shrublands of the Mojave Desert (Beatley 1974). *Coleogyne ramosissima* plants do not produce large fruit crops and abundant seeds in successive years even if rainfall is adequate (Pendleton et al. 1995). Similarly, low seed production may also apply to the associated woody taxa in the *C. ramosissima* shrubland despite favorable weather conditions occurring in some years. In this

Table 4. Soil physical and chemical characteristics (mean ± SE; n = 100 plots) at adjacent unburned areas and at various distances within burned areas in the *C. ramosissima* vegetation zone of Sandy Valley in July 1998. Within burned areas, seed density is shown at three distances from the fire edge. Soil samples were collected from the top 3 cm. Pore space and soil organic matter were expressed in percentages. Mean values in rows followed by different letters are significantly different at $P \leq 0.05$.

		Burned area		
Factor	Unburned area	8 m	300 m	600 m
Temperature (0 cm)	37.5 ± 0.16 a	39.7 ± 0.22 b	40.7 ± 0.25 b	40.2 ± 0.28 b
(3 cm)	36.4 ± 0.15 a	39.1 ± 0.15 b	39.4 ± 0.18 b	38.8 ± 0.17 b
Moisture (%)	1.1 ± 0.15 a	0.7 ± 0.04 b	0.6 ± 0.05 b	0.8 ± 0.07 b
pH	7.7 ± 0.04 a	8.0 ± 0.02 b	8.1 ± 0.03 b	8.0 ± 0.03 b
Bulk density (g/cm^3)	1.3 ± 0.08 a	1.4 ± 0.05 b	1.4 ± 0.07 b	1.4 ± 0.06 b
Compaction (kg/cm^2)	4.2 ± 0.25 a	5.0 ± 0.27 b	5.3 ± 0.29 b	5.4 ± 0.32 b
Pore space (%)	50.2 ± 3.83 a	46.0 ± 3.24 b	47.1 ± 4.34 b	45.7 ± 4.22 b
Organic matter (%)	4.1 ± 0.35 a	2.0 ± 0.20 b	2.3 ± 0.24 b	1.9 ± 0.21 b
Salinity (mmho/cm)	0.3 ± 0.04 a	0.4 ± 0.05 a	0.4 ± 0.03 a	0.4 ± 0.04 a

study, a combination of sharply contrasting mean annual precipitation and above average air temperatures following fire disturbance may partially explain the low soil seed densities and delayed seed germination of *C. ramosissima* and associated woody taxa.

Ecological Implications

The severe, lightning-induced fire in June 1987 created a unique set of postfire seed bank and edaphic conditions in Sandy Valley of southern Nevada. Fire caused a long-term removal of *C. ramosissima* and associated woody taxa. In addition to limited active dispersal mechanisms, extremely low soil seed densities, and adverse weather conditions, significant alterations in soil attributes following fire disturbance no longer favor the development of a seed bank for enhancing seed germination and seedling establishment of woody taxa. The lack of significant differences in seed density of woody species at various distances within the burned area seems to indicate an extremely slow recovery. Desert perennials are generally protected against environmental stochascity by a long life rather than by a persistent seed bank. However, the greater seed bank of *G. sarothrae* and *E. virginensis* may be a factor in their more successful response after fire disturbance. *Coleogyne ramosissima* plants may have an unusual method of seed bank development such as rodent caches. Ecological succession is stalled in the *C. ramosissima* vegetation zone. Whether a long recovery time reflects historic conditions of a dynamic ecosystem consisting of a diversity of different seral communities or whether it is simply an artifact of human intervention, a complete recovery time is yet to be determined. This study, however, provides one more part of the ultimate determination.

Acknowledgments

The valuable field assistance of Steven Lei, David Valenzuela, and Shevaun Valenzuela was gratefully acknowledged. Tim Rash of the Bureau of Land Management (BLM) provided valuable fire records and provided stimulating discussions. Critical review by David Charlet and an anonymous reviewer greatly improved the manuscript. The Department of Biology at the Community College of Southern Nevada (CCSN) provided logistical support.

Literature Cited

Analytical Software. 1994. Statistix 4.1, an interactive statistical program for microcomputers. St. Paul, Minnesota.

Barbour, M.G., J.H. Burk, and W.D. Pitts. 1987. Terrestrial plant Ecology. The Benjamin/Cumming Publishing Co., Inc., Menlo Park, California.

Beatley, J.C. 1974. Effects of rainfall and temperature on the distribution and behavior of *Larrea tridentata* (creosote-bush) in the Mojave Desert of Nevada. Ecology 55:245–261.

Beatley, J.C. 1975. Climates and vegetation pattern across the Mojave/Great Basin Desert transition of southern Nevada. Amer. Midland Nat. 93:53–70.

Beatley, J.C. 1980. Fluctuations and stability in climax shrub and woodland vegetation of the Mojave, Great Basin, and Transition Deserts of southern Nevada. Israel J. of Botany 28:149–168.

Bowns, J.E. 1973. An autecological study of blackbrush (*Colegyne ramosissima* Torr.) in southwestern Utah. Unpublished dissertation, Utah State University, Logan, Utah.

Bowns, J.E. and N.E. West. 1976. Blackbrush (*Coleogyne ramosissima* Torr.) on southern Utah rangelands. Department of Range Science, Utah State University. Utah Agricultural Experiment Station, Research Report 27.

Boyd, R.S. and G.D. Brum. 1983. Postdispersal reproductive biology of a Mojave desert population of *Larrea tridentata* (Zygophyllaceae). Amer. Midland Nat. 110:25–36.

Brown, D.E., and R.A. Minnich. 1986. Fire and changes in creosote bush scrub of the western Sonoran Desert, California. Amer. Midland Nat. 116:411–422.

Black, C.A., editor. 1965. Methods of soil analysis. Part I. Physical and minerological properties. Amer. Soc. of Agronomy, Madison, Wisconsin.

Callison, J., J.D. Brotherson, and J.E. Bowns. 1985. The effects of fire on the blackbrush (*Coleogyne ramosissima*) community of southwestern Utah. J. of Range Management 38:535–538.

Davidson, E. and M. Fox. 1974. Effects of off-road motorcycle activity on Mojave Desert vegetation and soil. Madrono 22:381–390.

Hausenbuiller, R.L. 1972. Soil Science. William C. Brown Company Publishers, Dubuque, Iowa.

Humphrey, R. R. 1974. Fire in the deserts and desert grassland of North America. *In*: T.T. Kozlowski and C.E. Ahlgren (eds.). Fire and Ecosystems. Academic Press, San Diego, California.

Korthuis, S.L. 1988. *Coleogyne ramosissima. In* W.C. Fisher (Comp.). The Fire Effects Information System (Data Base). U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Intermountain Fire Sciences Laboratory, Missoula, Montana. Magnetic tape reels; 9 track; 1600 bpi, ASCII with common LISP present.

Leck, M.A., V.T. Parker, and R.L. Simpson. 1989. Ecology of soil seed banks. Academic Press, Inc., San Diego, California.

Lei, S.A. and L.R. Walker. 1997. Classification and ordination of *Coleogyne* communities in southern Nevada. Great Basin Nat. 57:155–162.

Lei, S.A. 2000. Postfire vegetation recovery and soil properties in blackbrush (*Coleogyne ramosissima* Torr.) shrubland ecotones. Arizona-Nevada Acad. Sci. 32(2):105–115.

McLean, E.O. 1982. Soil pH and lime requirement. *In* C.A. Black, editor. Methods of soil analysis. American Society of Agronomy, Madison, Wisconsin, pp 199–209.

Minnich, R.A. 1995. Wildland fire and early postfire succession in joshua tree woodland and blackbrush scrub of the Mojave Desert of California, p. 99–106. *In* R.E. Reynolds and J. Reynolds (eds.) Ancient Surface of the east Mojave Desert, San Bernardino County Museum Association, San Bernardino, California.

Pendleton, B.K., S.E. Myer, and R.L. Pendleton. 1995. Blackbrush biology: insights after three years of long-term study. p. 223–227, *in* E.D. McArthur, J.S. Haley, and D.K. Mann, compilers. Proceedings: wildland shrub and arid land restoration symposium, General Technical Report INT-GTR-315, Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Raison, R.J. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformation: A review. Plant and Soil 51:73–108.

Reichman, O.J. 1975. Relation of desert rodent diets to available resources. J. of Mamm. 56:731–749.

Rhoades, J.D. 1982. Soluble salts. *In:* C.A. Black, editor. Methods of soil analysis. Amer. Soc. of Agronomy, Madison, Wisconsin. p. 176–173.

Scotter, G.W. 1963. Effects of forest fires on soil properties in northern Saskatchewan. Forestry Chronology 39:412–421.

Wright, H.A., and A.W. Bailey. 1982. Fire Ecology. United States and Southern Canada. John Wiley and Sons, New York.

Accepted for publication 28 January 2001.

Bull. Southern California Acad. Sci.
100(2), 2001, pp. 109–116

Helminths of Six Species of Colubrid Snakes from Southern California

Stephen R. Goldberg[1] and Charles R. Bursey[2]

[1]*Department of Biology, Whittier College, Whittier, California 90608*
[2]*Department of Biology, Pennsylvania State University, Shenango Campus, Sharon, Pennsylvania 16146*

Abstract.—Six species of colubrid snakes from California were examined for helminths: *Arizona elegans, Chionactis occipitalis, Masticophis flagellum, Masticophis lateralis, Phyllorhynchus decurtatus* and *Rhinocheilus lecontei.* One species of Trematoda, *Paralechriorchis syntomentera,* two species of Cestoda, *Oochoristica osheroffi* and *Mesocestoides* sp. (tetrathyridia), four species of Nematoda, *Physaloptera abjecta, Spauligodon goldbergi, Thubunaea iguanae,* and *Physaloptera* sp. (larvae) and one species of Acanthocephala represented by cystacanths (Oligacanthorhynchidae), were found. Nine new host records are reported.

Although 38 species of snakes are recorded for California (Brown 1997), few have been examined for helminths. There are reports of helminths for *Crotalus cerastes, C. ruber, C. viridis, Rhinocheilus lecontei,* and *Thamnophis elegans* collected in California (Voge 1953; Alexander and Alexander 1957; Mankau and Widmer 1977; Widmer and Specht 1992; Bursey et al. 1995; Goldberg et al. 1998). The purpose of this study was to examine 6 species of colubrid snakes from California for helminths: the glossy snake, *Arizona elegans;* western shovelnose snake, *Chionactis occipitalis;* coachwhip, *Masticophis flagellum;* striped racer, *Masticophis lateralis;* spotted leafnose snake, *Phyllorhynchus decurtatus;* and longnose snake, *Rhinocheilus lecontei.* Geographic ranges for these snakes are in Stebbins (1985). Of these 6 species, only *Masticophis flagellum* (from Georgia, Texas) has been examined for helminths (Harwood 1932; Reiber et al. 1940; Schad 1962; Conn and McAllister 1990).

Materials and Methods

One hundred fifty-nine individuals of six colubrid snake species: *Arizona elegans* (n = 43, mean snout-vent length [SVL] = 589 mm ± 205 SD, range = 238–930 mm), *Chionactis occipitalis* (n = 31, SVL = 258 mm ± 20 SD, range = 222–300 mm), *Masticophis flagellum* (n = 12, SVL = 861 mm ± 118 SD, range = 697–1104 mm), *Masticophis lateralis* (n = 14, SVL = 765 mm ± 136 SD, range = 520–963 mm), *Phyllorhynchus decurtatus* (n = 26, SVL = 357 mm ± 47 SD, range = 242–469 mm), and *Rhinocheilus lecontei* (n = 33, SVL = 590 mm ± 93 SD, range = 362–743 mm) were borrowed from the herpetology collection of the Natural History Museum of Los Angeles County (LACM), Los Angeles, California (accession numbers, Appendix 1). Eleven of 14 *Masticophis lateralis* (79%) were from the San Gabriel Mountains (34°18′N, 117°50′W) Los Angeles County, 3 (21%) were from the Puente Hills (34°01′N, 117°57′W) Los Angeles County, California. All individuals of the other five species were from desert areas in the Coachella Valley (33°50′N, 116°20′W) of Riverside County, California. Snakes were collected from 1951 to 1975.

The body cavity was opened by a longitudinal incision from vent to throat and the gastrointestinal tract was excised by cutting across the esophagus and rectum. The esophagus, stomach, and small and large intestines were slit longitudinally and examined under a dissecting microscope. Nematodes were examined and identified after clearing in a drop of concentrated glycerol. Trematodes, cestodes and acanthocephalans were regressively stained in hematoxylin and studied as whole-mounts in Canada balsam. Voucher helminths were deposited in the United States National Parasite Collection, (USNPC) Beltsville, Maryland (Appendix 2).

Results

One species of Trematoda, *Paralechriorchis syntomentera* (Sumwalt 1926) Bryd and Denton 1938; two species of Cestoda, *Oochoristica osheroffi* Meggitt 1934 and *Mesocestoides* sp. (as tetrathyridia); four species of Nematoda, *Physaloptera abjecta* Leidy 1856, *Spauligodon goldbergi* Bursey and McAllister 1996, *Thubunea iguanae* Telford 1965, *Physaloptera* sp. (third stage larvae); and one species of Acanthocephala represented by oligacanthorhynchid (proboscis short, globular; hooks in six spiral rows) cystacanths were found. Number of helminths, prevalence (infected snakes of a species divided by snake sample size expressed as a percentage), mean intensity (mean number of helminths per infected snake) and infection sites within the host are given in Table 1. Nine new host records are reported. *Arizona elegans* and *Masticophis lateralis* harbored five helminth species each; *Chionactis occipitalis* and *Rhinocheilus lecontei* harbored three; *Masticophis flagellum* harbored two and *Phyllorhynchus decurtatus* harbored one helminth species. Helminth community characteristics are given in Table 2.

Discussion

Arizona elegans, Chionactis occipitalis, Masticophis flagellum, Phyllorhynchus decurtatus and *Rhinocheilus lecontei* are sympatric in southern California and are found in dry, relatively open areas supporting chaparral, creosote bush, mesquite and sagebrush (Behler and King 1979). *Masticophis lateralis* prefers chaparral, open hardwood-pine forest in the mountains and is especially common around water (Behler and King 1979).

All helminths found in this study have been previously reported from snakes. *Paralechriorchis syntomentera* was originally described as *Zeugorchis syntomentera* by Sumwalt (1926) from the mouth cavity of *Thamnophis sirtalis* collected on San Juan Island, San Juan County, Washington. Byrd and Denton (1938) erected the genus *Paralechriorchis* for it and two closely related species. The life history of *P. syntomentera* was described by Ingles (1933) who experimentally infected young *Thamnophis ordinoides* collected at Berkeley, Alameda County, California through the ingestion of infected amphibians. Fantham and Porter (1954) have also reported *Thamnophis ordinoides* of Quebec, Canada to harbor *P. syntomentera. Masticophis lateralis* is a new host record.

Oochoristica osheroffi was originally described from *Pituophis melanoleucus* collected in Nebraska by Meggitt (1934). Alexander and Alexander (1957) described *Oochoristica crotalicola* from *Crotalus cerastes* and *C. viridis* of California; however, this cestode was synonymised with *O. osheroffi* by Widmer

Table 1. Number (N), prevalence (P), mean intensity (M ± SD), range (R), and site of infection for helminths of six colubrid snake species from California.

Helminth species Infection site	*Arizona elegans* (N = 43) P, M ± SD, R	*Chionactis occipitalis* (N = 31) P, M ± SD, R	*Masticophis flagellum* (N = 12) P, M ± SD, R	*Masticophis lateralis* (N = 14) P, M ± SD, R	*Phyllorhynchus decurtatus* (N = 26) P, M ± SD, R	*Rhinocheilus lecontei* (N = 33) P, M ± SD, R
Trematoda						
Paralechriorchis syntomentera esophagus	—	—	—	*7, 27, —	—	—
Cestoda						
Oochoristica osheroffi small intestine	*2, 2, —	—	—	*43, 2.8 ± 1.3, 1–5	—	—
Mesocestoides sp. (tetrathyrida) body cavity	12, 128.6 ± 135.0, 10–299	—	—	14, 54.5 ± 74.2, 2–107	—	6, 17.5 ± 21.9, 2–33
Nematoda						
Physaloptera abjecta stomach	*2, 1, —	—	—	—	—	—
Spauligodon goldbergi large intestine	—	*45, 12.6 ± 16.3, 1–58	—	—	—	—
Thubunaea iguanae stomach, small intestine	*9, 5.5 ± 6.1, 1–14	*23, 3.6 ± 4.3, 1–13	*8, 1, —	—	—	*23, 5.8 ± 6.0, 1–17
Physaloptera sp. (larvae) intestine	12, 4.4 ± 6.0, 1–15	23, 9.9 ± 6.0, 1–16	8, 1, —	43, 4.2 ± 4.6, 1–11	4, 2, —	6, 1.5 ± 0.7, 1–2
Acanthocephala						
oligacanthorhynchid cystacanths body cavity	—	—	—	7, 6, —	—	—

*Dew host record

Table 2. Characteristics of helminth communities of six species of snakes from California.

	Arizona elegans	*Chionactis occipitalis*	*Masticophis flagellum*	*Masticophis lateralis*	*Phyllorhynchus decurtatus*	*Rhinocheilus lecontei*
No. snakes examined	43	31	12	14	26	33
No. infected snakes (% infected)	13 (30)	21 (68)	2 (17)	10 (71)	1 (4)	10 (30)
No. helminth species	5	3	2	5	1	3
No. helminths	690	270	2	184	2	84
Mean no. helminths/infected snake	53.0 ± 102.3	12.9 ± 13.2	1	18.4 ± 33.1	2	8.4 ± 10.1
Mean no. helminth species/infected snake	1.2 ± 0.4	1.3 ± 0.5	1	1.6 ± 0.7	1	1.1 ± 0.3
Dominant helminth	*Mesocestoides* sp.	*S. goldbergi*	—	*Mesocestoides* sp.	—	*T. iguanae*
Proportion with 0 helminth species	0.70	0.32	0.83	0.29	0.96	0.70
Proportion with 1 helminth species	0.23	0.45	0.17	0.35	0.04	0.27
Proportion with 2 helminth species	0.07	0.23	0.00	0.29	0.00	0.03
Proportion with 3 helminth species	0.00	0.00	0.00	0.07	0.00	0.00

(1966). *Oochoristica osheroffi* has been reported in *Crotalus viridis* from Colorado and New Mexico (Widmer and Olsen 1967; Pfaffenberger et al. 1989). *Arizona elegans* and *Masticophis lateralis* represent new host records.

Tetrathyridia of *Mesocestoides* sp. are frequently found in snakes; McAllister et al. (1991) have summarized world occurrences. Tetrathyridia have been previously found in *Masticophis flagellum* from Texas by Conn and McAllister (1990) and from *Crotalus atrox, C. lepidus, C. molossus, C. pricei, C. ruber, C. scutulatus, C. tigris, C. viridis* and *Thamnophis elegans* from California (Voge 1953; Mankau and Widmer 1977; Widmer and Specht 1992; Bolette 1997a, 1997b; Goldberg and Bursey 1999). This is the first report of tetrathyridia in *Arizona elegans, Masticophis lateralis* and *Rhinocheilus lecontei.* Bolette (1997a) believed rattlesnakes serve as paratenic hosts.

Physaloptera abjecta was originally described from *Masticophis flagellum* (= *Psammophis flagelliformis*) from Pennsylvania by Leidy (1856). The identity of this snake is uncertain as *M. flagellum* does not occur in Pennsylvania (Conant and Collins 1998). *Physaloptera variegata* Reiber, Byrd and Parker 1940, described from a *Coluber constrictor* collected in Florida, was synonymized with *P. abjecta* by Morgan (1941). It has been reported from *Masticophis flagellum* of Georgia (Reiber et al. 1940) as well as the colubrids *Coluber constrictor, Heterodon platirhinos, Lampropeltis getula, Opheodrys* (= *Liopeltis*) *vernalis* and *Thamnophis sirtalis* from Georgia, Florida or Wisconsin and the anguid lizard, *Ophisaurus ventralis* from Georgia (Reiber et al. 1940; Morgan 1941; Mawson 1956). *Arizona elegans* is a new host record; California is a new locality record.

Spauligodon goldbergi was described from the ground snake, *Sonora semiannulata,* from Texas by Bursey and McAllister (1996). This is the second report of *Spauligodon goldbergi. Chionactis occipitalis* represents a new host record; California is a new locality record.

Thubunaea iguanae was originally described from the phrynosomatid lizard, *Sceloporus magister,* from Riverside County, California and was present in a variety of lizards collected by Telford (1965). *Arizona elegans, Chionactis occipitalis, Masticophis flagellum* and *Rhinocheilus lecontei* represent new host records. A related species, *Thubunaea cnemidophorus,* has been reported from *Crotalus cerastes, C. mitchellii* and *C. scutulatus* of southern Nevada (Babero and Emmerson 1974).

Third stage larvae of *Physaloptera* sp. were present in each of the species examined in this study and have also been reported in *M. flagellum* from Texas by Conn and McAllister (1990). The majority of the 16 species of *Physaloptera* from North America listed by Morgan (1941) have mammalian hosts. All species of *Physaloptera* require an insect intermediate host (Anderson 2000) and could be expected in any insectivore. Amphibians and reptiles harboring larvae of *Physaloptera* sp. but no adults are summarized in Goldberg et al. (1993). Because these larvae were found mainly in the intestine of the snakes examined, we believe they are a by-product of diet and will be passed in feces without further development. This is the first report of physalopteran larvae in *A. elegans, C. occipitalis, M. lateralis, P. decurtatus* and *R. lecontei.*

Oligacanthorhynchid cystacanths of acanthocephalans have previously been reported in *Rhinocheilus lecontei* from Riverside County, California as well as Arizona, Texas and Mexico (Goldberg et al. 1998). In addition, Bolette (1997b) reported oligacanthorhynchid cystacanths in *Rhinocheilus lecontei* collected in Arizona and provided a list of cystacanths from nine additional snake species. This is the first report of cystacanths in *Masticophis lateralis.*

The helminths found in this study fall into two categories: those requiring intermediate hosts, namely *Paralechriorchis syntomentera, Oochoristica osheroffi, Physaloptera abjecta, Thubunaea iguanae,* and the acanthocephalans; and those infecting directly by egg ingestion, namely *Mesocestoides* sp. and *Spauligodon goldbergi.* In all cases, it is an oral route of infection.

There is some dietary overlap in these snakes: *Arizona elegans* feeds mainly on lizards and rodents with a few birds and snakes; *Chionactis occipitalis* eats insects, spiders, scorpions and centipedes; *Masticophis flagellum* feeds on small mammals, birds, lizards, snakes, insects and carrion; *Masticophis lateralis* eats frogs, lizards, snakes, small mammals, birds and insects; *Phyllorhynchus decurtatus* feeds on small lizards and their eggs; *Rhinocheilus lecontei* feeds almost exclusively on lizards (Stebbins 1985; Rodriguez-Robles et al. 1999). Widmer and Olsen (1967) suggested that helminth infections can be transmitted to snakes when snakes eat infected arthropods or when they eat prey which has recently fed on infected arthropods. Likewise, ingestion of prey infected by a species of *Mesocestoides* or by *Spauligodon goldbergi* could introduce feces containing eggs of these species into a snake host with subsequent development of an infection.

Examination of other California snakes will be needed before helminth communities can be described and assigned. However, it is of interest to note that only *Masticophis lateralis* which is especially common in areas with water (Behler and King 1979) harbored *Paralechriorchis syntomentera,* a helminth requiring amphibians as intermediate hosts. All sympatric desert snakes eating lizards harbored *Thubunaea iguanae.* All six species contained third-stage larvae of *Physaloptera* sp., more likely a by-product of diet than potential infection. One desert snake species, *Arizona elegans,* and the non-desert species, *Masticophis lateralis,* harbored *Oochoristica osheroffi,* typically a parasite of rattlesnakes.

Acknowledgments

We thank David A. Kizirian (Natural History Museum of Los Angeles County) for permission to examine snakes and Cheryl Wong and Megan E. Lahti for assistance with dissections.

Literature Cited

Alexander, C. G., and E. P. Alexander. 1957. *Oochoristica crotalicola,* a new anoplocephalid cestode from California rattlesnakes. J. Parasitol. 43:365–366.

Anderson, R. C. 2000. Nematode parasites of vertebrates: Their development and transmission., 2nd edition, CABI Publishing, CAB International, Wallingford, Oxon, United Kingdom, xx + 650 pp.

Babero, B. B., and F. H. Emmerson. 1974. *Thubunaea cnemidophorus* in Nevada rattlesnakes. J. Parasitol. 60:595.

Behler, J. L., and F. W. King. 1979. The Audubon Society field guide to North American reptiles and amphibians. Alfred A. Knopf, New York, 743 pp.

Bolette, D. P. 1997a. First record of *Pachysentis canicola* (Acanthocephala: Oligacanthorhynchida) and the occurrence of *Mesocestoides* sp. tetrathyridia (Cestoidea: Cyclophyllidea) in the western diamondback rattlesnake, *Crotalus atrox* (Serpentes: Viperidae). J. Parasitol. 83:751–752.

———. 1997b. Oligacanthorhynchid cystacanths (Acanthocephala) in a long-nosed snake, *Rhinoch-*

eilus lecontei lecontei (Colubridae) and a Mojave rattlesnake, *Crotalus scutulatus scutulatus* (Viperidae) from Maricopa County, Arizona. Southwest. Nat. 42:232–236.

Brown, P. R. 1997. A field guide to snakes of California. Gulf Publishing Company, Houston, Texas, viii + 215 pp.

Bursey, C. R., S. R. Goldberg, and S. M. Secor. 1995. *Hexametra boddaertii* (Nematoda: Ascaridae) in the sidewinder, *Crotalus cerastes* (Crotalidae), from California. J. Helm. Soc. Wash. 62:78–80.

Bursey, C. R., and C. T. McAllister. 1996. *Spauligodon goldbergi* sp. n. (Nematoda: Pharyngodonidae) and other parasites of *Sonora semiannulata* (Serpentes: Colubridae) from New Mexico and Texas. J. Helm. Soc. Wash. 63:62–65.

Byrd, E. E., and J. F. Denton. 1938. New trematodes of the subfamily Reniferinae, with a discussion of the systematics of the genera and species assigned to the subfamily group. J. Parasitol. 24: 379–401.

Conant, R., and J. T. Collins. 1998. A field guide to reptiles and amphibians: Eastern and central North America, third edition, Houghton Mifflin Company, Boston, xviii + 616 pp.

Conn, D. B., and C. T. McAllister. 1990. An aberrant acephalic metacestode and other parasites of *Masticophis flagellum* (Reptilia: Serpentes) from Texas. J. Helminthol. Soc. Wash. 57:140–145.

Fantham, H. B., and A. Porter. 1954. The endoparasites of some North American snakes and their effects on the Ophidia. Proc. Zool. Soc. London 123:867–898.

Goldberg, S. R., and C. R. Bursey. 1999. *Crotalus lepidus* (Rock Rattlesnake), *Crotalus molossus* (Blacktail rattlesnake), *Crotalus pricei* (Twin-spotted rattlesnake), *Crotalus tigris* (Tiger rattlesnake). Endoparasites. Herpetol. Rev. 30:44–45.

Goldberg, S. R., C. R. Bursey, and H. J. Holshuh. 1998. Prevalence and distribution of cystacanths of an oligacanthorhynchid acanthocephalan from the longnose snake, *Rhinocheilus lecontei* (Colubridae), in southwestern North America. J. Helminthol. Soc. Wash. 65:262–265.

Goldberg, S. R., C. R. Bursey, and R. Tawil. 1993. Gastrointestinal helminths of the western brush lizard, *Urosaurus graciosus graciosus* (Phrynosomatidae). Bull. Southern Calif. Acad. Sci. 92: 43–51.

Harwood, P. D. 1932. The helminths parasitic in the amphibia and reptilia of Houston, Texas, and vicinity. Proc. U.S. Natl. Mus. 81:1–76.

Ingles, L. G. 1933. Studies on the structure and life-history of *Zeugorchis syntomentera* Sumwalt, a trematode from the snake *Thamnophis ordinoides* from California. Univ. Calif. Publ. Zool. 39: 163–178.

Leidy, J. 1856. A synopsis of entozoa and some of their ecto-congeners observed by the author. Proc. Acad. Nat. Sci. Philadelphia 42–58.

Mankau, S. K., and E. A. Widmer. 1977. Prevalence of *Mesocestoides* (Eucestoda: Mesocestoididea) tetrathyridia in southern California reptiles with notes on the pathology in the Crotalidae. Jap. J. Parasitol. 26:256–259.

Mawson, P. M. 1956. *Physaloptera variegata* Reiber, Byrd and Parker, 1940 from three species of reptiles. Can. J. Zool. 34:75–76.

McAllister, C. T., D. B. Conn, P. S. Freed, and D. A. Burdick. 1991. A new host and locality record for *Mesocestoides* sp. tetrathyridia (Cestoidea: Cyclophyllidea), with a summary of the genus from snakes of the world. J. Parasitol. 77:329–331.

Meggitt, F. J. 1934. On some tapeworms from the bullsnake (*Pityopis sayi*), with remarks on the species of the genus *Oochoristica* (Cestoda). J. Parasitol. 20:181–189.

Morgan, B. B. 1941. A summary of the Physalopterinae (Nematoda) of North America. Proc. Helm. Soc. Wash. 8:28–30.

Pfaffenberger, G. S., N. M. Jorgensen, and D. D. Woody. 1989. Parasites of prairie rattlesnakes (*Crotalus viridis viridis*) and gopher snakes (*Pituophis melanoleucus sayi*) from the eastern high plains of New Mexico. J. Wild. Dis. 25:305–306.

Reiber, R. J., E. E. Byrd, and M. V. Parker. 1940. Certain new and already known nematodes from Amphibia and Reptilia. Lloydia 3:125–144.

Rodríguez-Robles, J. A., C. J. Bell, and H. W. Greene. 1999. Food habits of the glossy snake, *Arizona elegans,* with comparisons to the diet of sympatric long-nosed snakes, *Rhinocheilus lecontei.* J. Herp. 33:87–92.

Schad, G. A. 1962. Studies on the genus *Kalicephalus* (Nematoda: Diaphanocephalidae) II. a taxonomic revision of the genus *Kalicephalus* Molin, 1861. Can. J. Zool. 40:1035–1165.

Stebbins, R. C. 1985. A field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston, xiv + 336 pp.

Sumwalt, M. 1926. Trematode infestation of the snakes of San Juan Island, Puget Sound. Washington University Studies 13:73–101.

Telford, S. R., Jr. 1965. A new species of *Thubunaea* (Nematoda: Spiruroidea) from California lizards. Jap. J. Exp. Med. 35:111–114.

Voge, M. 1953. New host records for *Mesocestoides* (Cestoda: Cyclophyllidea) in California. Am. Midl. Nat. 49:249–251.

Widmer, E. A. 1966. Synonymy of *Oochoristica crotalicola* Alexander and Alexander, 1957. Bull. Wild. Dis. Assoc. 2:82–84.

Widmer, E. A., and O. W. Olsen. 1967. The life history of *Oochoristica osheroffi* Meggitt, 1934 (Cyclophyllidea: Anoplocephalidae). J. Parasitol. 53:343–349.

Widmer, E. A., and H. D. Specht. 1992. Isolation of asexually proliferative tetrathyridia (*Mesocestoides* sp.) from the southern Pacific rattlesnake (*Crotalus viridis helleri*) with additional data from two previous isolates from the Great Basin fence lizard (*Sceloporus occidentalis longipes*). J. Parasitol. 78:921–923.

Accepted for publication 19 September 2000.

Appendix 1

Museum numbers (LACM) from the Natural History Museum of Los Angeles County for six species of colubrid snakes from California.

Arizona elegans (n = 43) 102030–102035, 102037–102063, 102101–102107, 102109–102111.

Chionactis occipitalis (n = 31) 42410, 52292, 52300, 52301, 52306, 52311, 52325, 52327, 52344, 52354, 52361, 52369, 52373, 52378, 52379, 52387–52389, 52401, 52405, 52425, 52430, 63625, 102757–102760, 102762, 102768, 122099, 122100.

Masticophis flagellum (n = 12) 103136, 103138, 103149, 103150, 103153, 103164, 103165, 103172, 103174, 103176, 103178, 103182.

Masticophis lateralis (n = 14) 027794, 027795, 027797, 052540, 052542, 075211, 111203, 111204, 111207, 111210, 111213, 111215, 111216, 111218.

Phyllorhynchus decurtatus (n = 26) 102868, 102874, 102904, 102910, 102913, 102921–102923, 102925–102930, 102934, 102935, 102937, 102939, 102943, 102949–102951, 115876, 115877, 133896, 133897.

Rhinocheilus lecontei (n = 33) 102622, 102624, 102627, 102630–102632, 102634, 102636, 102638, 102639, 102641–102643, 102645–102647, 102655, 102656, 102660–102667, 102669, 102672–102677.

Appendix 2

Helminths deposited in the United States National Parasite Collection (USNPC) for six species of colubrid snakes from California.

Arizona elegans: Oochoristica osheroffi (90583); *Mesocestoides* sp. (90425); *Physaloptera abjecta* (90426); *Thubunaea iguanae* (90427); *Physaloptera* sp. (90428). *Chionactis occipitalis: Spauligodon goldbergi* (90429); *Thubunaea iguanae* (90430); *Physaloptera* sp. (90431). *Masticophis flagellum: Thubunaea iguanae* (90432); *Physaloptera* sp. (90433).

Masticophis lateralis: Paralechriorchis syntomentera (90434); *Oochoristica osheroffi* (90435); *Mesocestoides* sp. (90436); *Physaloptera* sp. (90437); oligacanthorhynchid cystacanths (90438).

Phyllorhynchus decurtatus: Physaloptera sp. (90439). *Rhinocheilus lecontei: Mesocestoides* sp. (90441); *Thubunaea iguanae* (90440); *Physaloptera* sp. (90442).

Bull. Southern California Acad. Sci.
100(2), 2001, pp. 117–122

Helminths of the California Treefrog, *Hyla cadaverina* (Hylidae), from Southern California

Stephen R. Goldberg[1] and Charles R. Bursey[2]

[1]*Department of Biology, Whittier College, Whittier, California 90608*
[2]*Department of Biology, Pennsylvania State University, Shenango Campus, Sharon, Pennsylvania 16146*

Abstract.—Ninety-one California treefrogs, *Hyla cadaverina,* from three counties in southern California (Los Angeles, Orange, Riverside) were examined for helminths. The trematode, *Langeronia burseyi,* and metacercariae of *Alaria* sp., *Fibricola* sp., and *Gorgoderina* sp.; the cestode, *Distoichometra bufonis,* and two species of nematodes, *Rhabdias ranae* and larvae of *Physaloptera* sp., were found. Helminth distribution patterns were found to be patchy; no two counties exhibited the same combination of helminth species.

The California treefrog, *Hyla cadaverina* Cope 1866, is known from the mountains of southern California to northern Baja California from elevations near sea level to around 2290 m (Stebbins 1985). To our knowledge, there is one report (Dailey and Goldberg 2000) of helminths from this species. The purpose of this paper is to analyze helminth infracommunities of *H. cadaverina* from the northern portion of its range: Los Angeles County, Orange County and Riverside County, California.

Materials and Methods

Ninety-one *H. cadaverina* (Los Angeles County: N = 34, snout-vent length [SVL] = 32 mm ± 4 SD, range = 25–41 mm, collected 1963–1965; Orange County: N = 39, SVL = 37 mm ± 5 SD, range = 17–45 mm, collected 1960–1972; Riverside County: N = 18, SVL = 28 mm ± 6 SD, range = 21–42 mm, collected 1964–1971) were borrowed from the Natural History Museum of Los Angeles County (LACM) and examined for helminths (accession numbers in appendix). The body cavity of each treefrog was opened by a longitudinal incision and the gastrointestinal tract was removed and slit longitudinally. The esophagus, stomach, small intestine, large intestine as well as lungs, urinary bladder, coelom and liver were searched for helminths with a dissecting microscope. Nematodes were placed in a drop of undiluted glycerol on a glass slide and allowed to clear for study with a compound microscope. Nematodes were identified from these slides. Trematodes and cestodes were stained in hematoxylin and mounted in balsam for identification. Numbers of individuals for each species of helminth were recorded for each host. Prevalence (the percentage of infected frogs), mean intensity (the mean number of helminths per infected frog), abundance (the number of individuals of a helminth species divided by the number of hosts examined) and species richness (the number of helminth species per infected frog) were determined. Prevalences of infection for male and female frogs were compared by the chi-square test (χ^2), numbers of helminths per male and female hosts were evaluated by the Kruskal-Wallis test and correlation analysis (*r*) was used to relate intensity of infection to age of host (as estimated by SVL). A discussion of measures of analyses for community structure can be found in Brower et al. (1998). Of these, measures selected for evaluation of the component helminth community structure were species richness, Simpson dominance, and Simpson diversity. For evaluation of helminth infracommunity structure, mean number of helminth individuals per host, mean number of helminth species per host and Brillouin's index were used. For community similarity, the Jaccard coefficient, percentage of similarity, and Morisita's index were used.

Results and Discussion

Gravid individuals of one species of trematode, (*Langeronia burseyi* Dailey and Goldberg 2000); one species of cestode, (*Distoichometra bufonis* Dickey 1921); and one species of nematode, (*Rhabdias ranae* Walton 1929), were found. Metacercariae of three species of trematodes, (*Alaria* sp., *Fibricola* sp. and *Gorgoderina* sp.), and larvae of one species of nematode, (*Physaloptera* sp.), were found. Voucher specimens were placed in vials of 70% ethanol and deposited in the United States National Parasite Collection (Appendix).

Twenty-eight treefrogs (31%) were found to harbor 590 helminths ($\bar{X} = 21 \pm 42$ SD per infected treefrog), of which 469 (79%) were larvae of species not capable of completing their life cycles in anurans. These include *Alaria* sp., *Fibricola* sp. and *Physaloptera* sp., (see Smyth and Smyth 1980; Goldberg et al. 1993). Mean helminth species richness for infected treefrogs was 1.2 ± 0.5 SD (range = 1–3 species). Seventeen of 53 male treefrogs (32%) harbored 354 helminths; 11 of 38 female treefrogs (29%) harbored 236 helminths. Neither prevalence of helminth infection nor number of helminths per host was significantly different between male and female treefrogs ($\chi^2 = 0.10$, 1 df, $P > 0.05$; Kruskal Wallis test = 0.43, $P > 0.05$, respectively). Twenty-four treefrogs (26%) harbored a single species of helminth; 3 (3%) harbored 2 species; and 1 individual (1%) harbored three species. The smallest infected frog measured 22 mm SVL; there was a positive correlation between number of helminths (all species combined) and SVL ($r = 0.34$, $P = 0.080$). Number, prevalence and mean intensity of helminths by county are given in Table 1.

Similarity characteristics of the helminth component communities are summarized in Table 2. The Jaccard coefficient is based upon species presence in a community and ranges from 0 (no species found in both communities) to 1.0 (all species found in both communities). Morisita's index considers the number of species, the number of individuals, as well as the proportion of the total represented by each species and ranges from 0% (no similarity) to 1.0 (identical). Percentage of similarity is based upon species abundance and ranges from 0% (no species found in both communities) to 100% (same species found in both communities at similar abundances). No two counties exhibited the same combinations of helminth species. In this study (Table 1), the helminth communities from Los Angeles County and Orange County are shown to have two species in common, the helminth communities from Los Angeles County and Riverside County have one species in common; however, helminth communities from Orange County and Riverside County have no species in common.

Infracommunity structure is presented in Table 3. Brillouin's index is used in

Table 1. Infection sites, number of helminths (N), prevalence (P), and mean intensity (MI ± 1 SD) for helminths from *Hyla cadaverina* by county from southern California.

Order Helminth	Infection site	Los Angeles County			Orange County			Riverside County		
		N	P	MI ± 1 SD	N	P	MI + 1 SD	N	P	MI ± 1 SD
Trematoda										
Langeronia burseyi	Large intestine	—	—	—	83	3	83	—	—	—
Alaria sp. (mesocercaria)	Body cavity	—	—	—	—	—	—	1	5	1
Fibricola sp. (metacercaria)	Body cavity, muscles	141	18	23.5 ± 29.3	—	—	—	—	—	—
Gorgoderina sp. (metacercaria)	Body cavity, skin	228	21	32.5 ± 53.6	86	5	43.0 ± 52.3	—	—	—
Cestoda										
Distoichometra bufonis	Small intestine	—	—	—	—	—	—	12	17	4.0 ± 3.6
Nematoda										
Rhabdias ranae	Lung	2	6	1	—	—	—	24	50	2.7 ± 2.2
Physaloptera sp. (larvae)	Stomach	3	3	3	10	5	5.0 ± 2.8	—	—	—

Table 2. Jaccard coefficient, Morisita's index and percentage of similarity for helminth communities of *Hyla cadaverina* by county from southern California.

	Orange County	Riverside County
Jaccard coefficient		
Los Angeles County	0.40	0.17
Orange County		0
Morisita's index		
Los Angeles County	0.61	0.01
Orange County		0
Percentage of similarity		
Los Angeles County	48.8	0.50
Orange County		0

a relative fashion to determine which species assemblages are more or less diverse than others and is based upon relative abundance with larger values indicating evenness of distribution across species. Simpson diversity is based upon abundance with larger values indicating evenness of distribution of individuals across species. Simpson dominance is also based upon abundance with larger values indicating aggregation of most individuals into one or a few species. Based upon Brillouin's index, the helminth infrapopulation collected in Orange County has the most even distribution. Simpson diversity index indicates that Los Angeles County and Riverside County have similar diversities and are less diverse than the infracommunity in Orange County. Likewise, most helminths in the infracommunities of Los Angeles County and Riverside County belong to one species (Simpson dominance index).

Except for *Langeronia burseyi* which is presently known only from *H. cadav-*

Table 3. Diversity characteristics of the helminth infracommunities for *Hyla cadaverina* by county from southern California.

Characteristics	Los Angeles County	Orange County	Riverside County
No. treefrogs examined	34	39	18
Mean SVL ± SD, range (mm)	32 ± 4	37 ± 5	28 ± 6
No. treefrogs infected	11	4	12
Prevalence (as %)	32	10	67
No. helminths	374	179	37
Mean intensity ± SD	33.9 ± 45.6	44.7 ± 78.8	3.1 ± 2.4
Mean abundance ± SD	11.0 ± 29.8	4.6 ± 26.1	2.1 ± 2.5
Mean species richness ± SD	1.3 ± 0.7	1.3 ± 0.5	1.1 ± 0.3
No. helminth species	4	3	3
Proportion with 0 helminth species	0.67	0.89	0.33
Proportion with 1 helminth species	0.24	0.08	0.61
Proportion with 2 helminth species	0.06	0.03	0.06
Proportion with 3 helminth species	0.03	0.00	0.00
Proportion with 4 helminth species	0.00	—	—
No. helminths species maturing in anurans	2	1	1
Brillouin's index	0.31	0.37	0.12
Simpson diversity (D_s)	0.49	0.55	0.49
Simpson dominance (d_s)	0.51	0.45	0.51

erina collected in Orange County (Dailey and Goldberg 2000), none of the helminth species found in this study was unique to *H. cadaverina.* However, this is the first record of *H. cadaverina* as a host for *D. bufonis* and *R. ranae* as well as the first report of *Alaria* sp., *Fibricola* sp., *Gorgoderina* sp., and *Physaloptera* sp. in *H. cadaverina.* Species of *Alaria* and *Fibricola* utilize mammals as final hosts, species of *Gorgoderina* utilize anurans as final hosts; metacercariae of all 3 species are commonly found in frogs (Smyth and Smyth 1980). *Distoichometra bufonis* is a common parasite of anurans (Brooks 1976) as is *R. ranae* (see Baker 1987). Larvae of *Physaloptera* spp., usually parasites of lizards and mammals, have been reported from anurans (Anderson 2000).

Of the 7 helminth species found in this study, 4 species are capable of completing their life cycles in anurans. Individuals of *Gorgoderina* require bivalve intermediate hosts and aquatic insects or tadpoles serve as second intermediate hosts (Smyth and Smyth 1980). When infected tadpoles or insect larvae are eaten by frogs, excystment takes place in the stomach and migration to the kidneys and bladder occurs (Smyth and Smyth 1980). We cannot speculate whether the *Gorgoderina* metacercariae found in the present study would have migrated to the kidneys or bladder to complete development or if *H. cadaverina* was acting as a paratenic (transport) host. The life cycle of *L. burseyi* is unknown but other lecithodendriid trematodes have been shown to utilize snails as intermediate hosts (Schell 1970). Likewise, the life cycle of *D. bufonis* is unknown, but Joyeux (1927) regards the life cycle of nematotaeniid cestodes to be direct, i.e., without an intermediate host and infection of a new host occurs through ingestion of cestode eggs. *Rhabdias ranae* has a direct life cycle and infection occurs by integumental penetration (Anderson 2000). Of the non-anuran parasites, species of *Physaloptera* utilize insect intermediate hosts and adults occur mainly in stomachs of reptiles, birds and mammals (Anderson 2000); larvae might be expected in any insectivorous host. Miracidia of *Alaria* sp. (definitive host = carnivore) and *Fibricola* sp. (definitive host = mouse, raccoon) utilize snails as intermediate hosts (Smyth and Smyth 1980). Cercariae of both *Alaria* sp. and *Fibricola* sp. may penetrate the skin of either tadpoles or frogs (Hayden 1969; Pearson 1961).

It would be of interest to know which helminth species infect sympatric anurans and whether there is recruitment of helminths from one locality to another. Periodic visits to water are the most likely time for infection by *L. burseyi, Alaria* sp., *Fibricola* sp., *Gorgoderina* sp. and *R. ranae.* Distribution patterns of definitive hosts, as well as intermediate hosts, may help explain the presence or absence of these helminths in the localities examined. Feeding behavior would be a more important consideration for infection by *D. bufonis* and *Physaloptera* sp. Presence of these helminths in *H. cadaverina* is, no doubt, the result of patchy distribution of the particular helminth species.

Acknowledgment

We thank David A. Kizirian (Natural History Museum of Los Angeles County) for permission to examine *H. cadaverina.*

Literature Cited

Anderson, R. C. 2000. Nematode parasites of vertebrates: Their development and transmission. 2nd edition. CABI Publishing, CAB International, Wallingford, Oxon, U.K. 650 pp.

Baker, M. R. 1987. Synopsis of the Nematoda parasitic in amphibians and reptiles. Mem. Univ. Newfoundland, Occas. Pap. Biol., 11:1–325.

Brooks, D. R. 1976. Parasites of amphibians of the Great Plains. Part 2. Platyhelminths of amphibians in Nebraska. Bull. Univ. Nebraska St. Mus., 10:65–92.

Brower, J. E., J. H. Zar, and C. N. von Ende. 1998. Field and laboratory methods for general ecology, 4th edition. McGraw-Hill, Boston, Massachusetts. xi + 273 pp.

Dailey, M. D., and S. R. Goldberg. 2000. *Langeronia burseyi* sp. n. (Trematoda: Lecithodendriidae) from the California treefrog, *Hyla cadaverina* (Anura: Hylidae), with revision of the genus *Langeronia* Caballero and Bravo-Hollis, 1949. Comp. Parasitol., 67:165–168.

Goldberg, S. R., C. R. Bursey and R. Tawil. 1993. Gastrointestinal helminths of the western brush lizard, *Urosaurus graciosus graciosus* (Phrynosomatidae). Bull. So. Calif. Acad. Sci., 92: 43–51.

Hayden, D. W. 1969. Alariasis in a dog. J. Amer. Vet. Med. Assoc., 155:889–891.

Joyeux, C. 1927. Recherches sur la faune helminthologique Algérienne (cestodes et trématodes). Arch. de l'Institut Pasteur d'Algérie, 5:509–528.

Pearson, J. C. 1961. Observations on the morphology and life cycle of *Neodiplostomum intermedium* (Trematoda: Diplostomatidae). Parasitology, 51:133–172.

Schell, S. C. 1970. How to know the trematodes. W. C. Brown Co., Dubuque, Iowa, vii + 355 pp.

Smyth, J. D., and M. M. Smyth. 1980. Frogs as host-parasite systems I. The MacMillan Press, Ltd., London, ix + 112 pp.

Stebbins, R. C. 1985. A field guide to western reptiles and amphibians. Houghton Mifflin Company, Boston, xiv + 336 pp.

Accepted for publication 21 December 2000.

Appendix

Hyla cadaverina borrowed from the Natural History Museum of Los Angeles County (LACM) by California County. Los Angeles County: 12263, 12265–12273, 12275–12280, 12283–12285, 12287–12294, 114170–114176; Orange County: 88837, 88854, 88881, 88882, 88894, 88895, 88905, 88907, 88918, 88921, 88923, 88927, 88930–88933, 88935, 88937, 88941, 88942, 88946, 88953–88956, 88958–88960, 88962–88969, 114182–114184; Riverside County: 114185, 114187–114198, 114200–114204. Helminths from *Hyla cadaverina* deposited in the United States Parasite Collection, USNPC, Beltsville, Maryland: *Langeronia burseyi* 90644; *Alaria* sp. 90645; *Fibricola* sp. 90646; *Gorgoderina* sp. 90647; *Distoichometra bufonis* 90648; *Rhabdias ranae* 90649; *Physaloptera* sp. 90650.

Bull. Southern California Acad. Sci.
100(2), 2001, pp. 123–127

A New North Pacific *Heterochone* Transferred from *Aphrocallistes* (Porifera: Hexactinellida)

Henry M. Reiswig

Redpath Museum and Department of Biology, McGill University,
859 Sherbrooke St. W., Montreal, Quebec, Canada H3A 2K6
email: cxhr@musica.mcgill.ca

Abstract.—A hexactinellid sponge specimen from southern California, determined as a member of the genus *Heterochone,* was found to be conspecific with *Aphrocallistes beatrix incognitus,* a form previously described from the Okhotsk Sea by Koltun (1967). The taxon is redescribed and reassigned as a new combination, *Heterochone incognitus* (Koltun). It represents an addition to the North American Pacific fauna. The simple zoological diagnosis of *Heterochone* is: Aphrocallistidae with atrialia as pinular hexactins.

The deep-water marine fauna of the Pacific Coast of North America is poorly known primarily owing to avoidance of the region by the major oceanographic expeditions of the late 1900's. During an ongoing survey of California collections by myself and coworkers, with the aim of producing an updated guide to the Porifera of California, we encountered a hexactinellid sponge from southern California unknown to the region (last summarized by de Laubenfels 1932). The specimen is the third and, although imperfect, the best preserved specimen of a species known to date as *Aphrocallistes beatrix incognitus;* it has been recorded only from the Okhotsk Sea, eastern Russia (Koltun 1967). The severely damaged condition of the earlier specimens is likely cause for the original incorrect generic assignment, which is here resolved and corrected.

Materials and Methods

The specimen was obtained on loan from the Benthic Invertebrate Collection of Scripps Institute of Oceanography, La Jolla, California (SIO). After photographing the specimen, small pieces of dermal and atrial surfaces were wholemounted in Canada balsam for light microscopy and digested in hot nitric acid for spicule cleaning. Cleaned spicules were either mounted directly in balsam on slides or retained on nitrocellulose filters which were cleared and mounted on slides. Spicules and body apertures were measured by microscope-coupled digitizer. Spicule drawings were made directly from video-captured images. Data in text are given as: minimum-*mean*-maximum of 25 measurements.

Systematics

Class Hexactinellida Schmidt, 1870
Subclass Hexasterophora Schulze, 1886
Order Hexactinosa Schrammen, 1903
Family Aphrocallistidae Gray, 1867
Genus *Heterochone* Ijima, 1927

Diagnosis.—Aphrocallistidae with atrialia as pinular hexactins.

Type species.—*Chonelasma calyx* Schulze, 1886

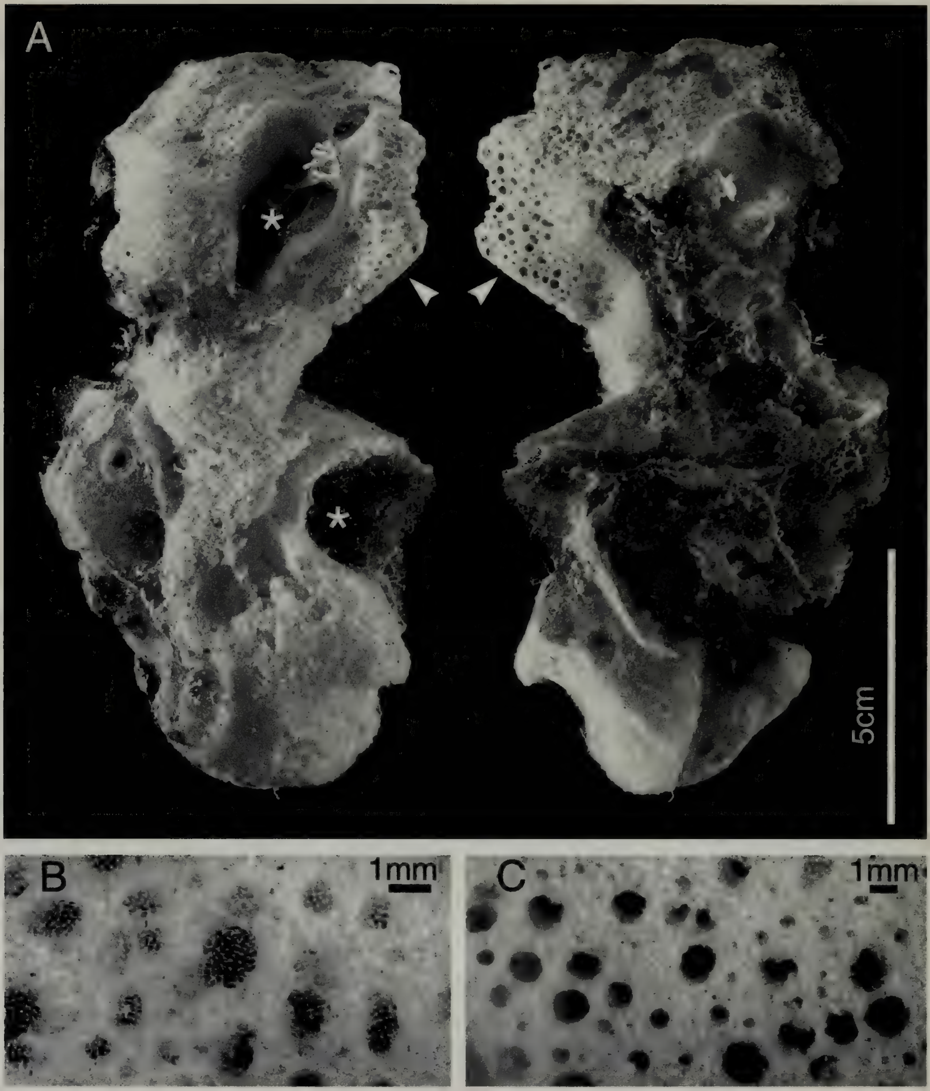


Fig. 1. *Heterochone incognitus* specimen SIO P 592. A, presumed lower (right) and upper (left) surfaces of the lobate fragment, with bases of two funnels indicated by asterisks and intact portion of funnel wall indicated by arrowheads. B, dermal surface with intact pinule lattice covering entire surface, including entrances to diarhysial channels. C, atrial surface with open, uncovered apertures of diarhysial channels.

Remarks.—Upon his erection of *Heterochone,* Ijima (1927) provided an extensive comparison of the new genus with its only sister genus, *Aphrocallistes,* but did not provide a diagnosis. Reid (1963), aware of Ijima's action, characterized the genus by body form, a strategy perhaps necessary for paleontological use but insufficient for zoological application. Koltun (1967) was apparently unaware of Ijima's formation of *Heterochone,* perhaps because it was mistakenly omitted from the final list of Ijima's (1927) publication (Reiswig 1990). The short, new diagnosis provided here differentiates *Heterochone* (with hexactine atrialia) from *Aphrocallistes* (with diactine atrialia).

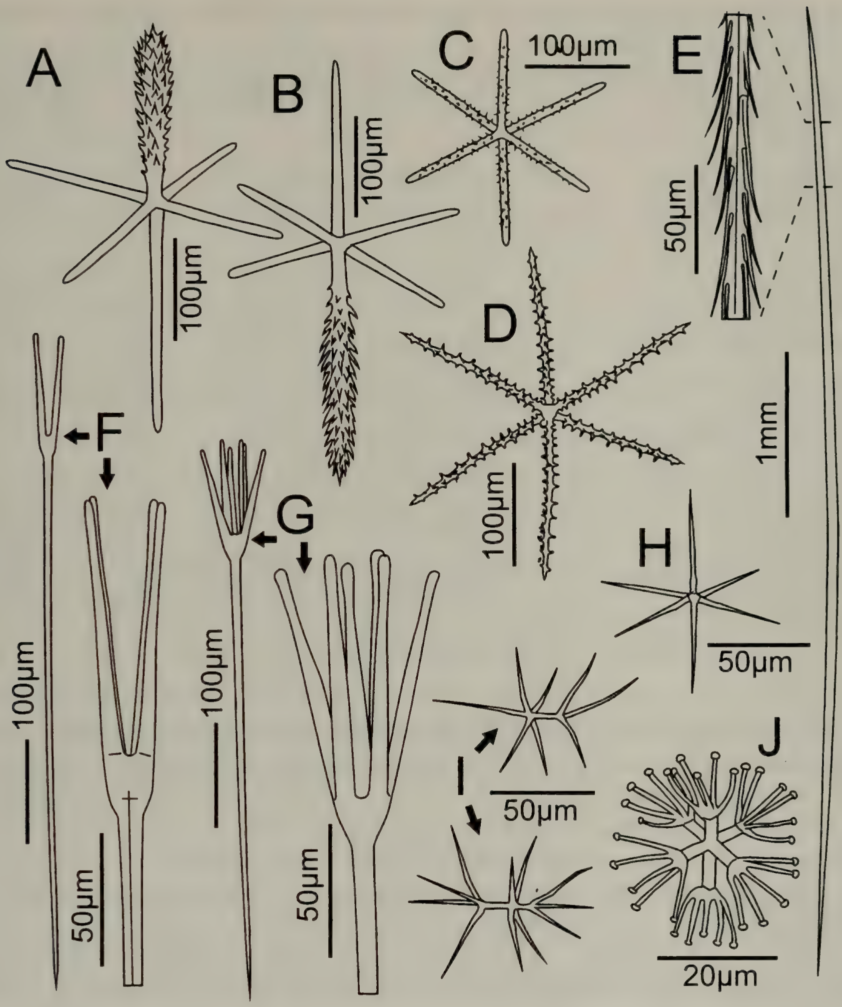


Fig. 2. Spicules of *Heterochone incognitus* specimen SIO P 592. A, dermal pinular hexactin. B, atrial pinular hexactin. C, small moderately-spined hexactin. D, larger coarsely-spined hexactin. E, uncinate, entire and magnified segment. F, narrow scopule with 4 tines. G, divergent scopule with 6 tines. H, oxyhexactine microsclere. I, two hemioxyhexasters with branching restricted to rays of the major axis. J, discohexaster.

Heterochone incognitus (Koltun, 1967)
Figs. 1–2, Table 1.

Synonymy.—Aphrocallistes beatrix incognitus Kotun, 1967: 60, Fig. 39.

Holotype.—Zoological Institute, Russian Academy of Science (Leningrad) N 16362 (2 fragments), 148°57′E, 44°41′N, 780m, RV ‘Vitiaz’ stn. 5640 (not examined).

Material examined.—SIO P 592, in alcohol, 118°53.6′W, 33°20.4′N. 1165–958 m depth, 11 Dec. 1971, RV ‘Thomas Washington’, col. Mathews.

Body and framework.—Specimen a massive irregular fragment, 13.4 cm × 6.9 cm × 4.0 cm, as part of basal region without attachment site; dead skeletal frame-

Table 1. Spicule measurements of *Heterochone incognitus,* SIO P 592 with comparison data from Okhotsk Sea specimens of Koltun, 1967.

Item measured	Mean ± s.d.	Range	N	Koltun, 1967
Dermal pinule A				
pinulus length (μm)	15 ± 24	88–222	100	120–165
tangential ray length (μm)	156 ± 22	104–227	100	99–154
proximal ray length (μm)	304 ± 155	68–728	100	159–264
Gastral pinule B				
pinulus length (μm)	198 ± 47	85–280	25	n.r.
tangential ray length (μm)	170 ± 37	104–247	25	n.r.
proximal ray length (μm)	135 ± 33	65–193	25	n.r.
Scopule F length (μm)	606 ± 84	420–756	25	412–660*
Scopule G length (μm)	537 ± 103	369–751	25	412–660*
Hexactin D ray length (μm)	216 ± 47	146–341	25	n.r.
Hexactin C ray length (μm)	172 ± 41	100–278	25	n.r.
Uncinate length (mm)	5.4 ± 0.9	3.6–7.1	22	1.0–4.0
width (μm)	24 ± 5	12–35	50	13–32
Oxyhexactin diameter (μm)	92 ± 16	64–126	25	66–121
Hemioxyhexaster diameter (μm)	100 ± 19	65–129	25	n.m.
Discohexaster diameter (μm)	28.8 ± 5.8	21.2–44.3	25	38

* Scouple types not measrued separately; n.r. = not reported; n.m. = not measured.

work on presumed lower side; 2 major depressions interpreted as bases of mostly missing funnel-form body extensions on opposite presumed upper side (Fig. 1A); surface even and compacted but edge of upper funnel with small region of intact body wall (Fig. 1A, arrows); wall 1 cm thick penetrated by radial diarhyses (skeletal channels of dictyonal framework) passing from dermal to atrial surface; dermal surface entirely covered by rectangular lattice of loose pinular hexactins of 149-*183*-235 μm mesh (Fig. 1B); dermal openings of diarhyses 0.44-*1.07*-1.88 mm diameter and irregulary distributed; atrial surface lined by compact felt of pinular hexactins not forming a rectangular lattice; atrial apertures of diarhyses 0.27-*0.94*-1.74 mm diameter, irregularly distributed, uncovered and open (Fig. 1C); dictyonal framework typically aphrocallistid (with diarhyses) with beams partly smooth and partly sparsly spined, 49-*88*-188 μm in thickness; meshes 3- and 4-sided, very irregular with sides 183-*483*-1059 μm.

Spicules.—Spicule form and dimensions are summarized in Fig. 2 and Table 1. Megascleres: Dermal and atrial pinular hexactins (Fig. 2A–B) are similar but proximal rays of dermal forms have greater length range; parenchymal hexactins occur in larger coarsly spined form (Fig. 2D) and smaller moderately spined form (Fig. 2C); scopules with micro-thorned tines occur in 2 forms in both surfaces: form with 4 tines and small (10°) angular spread (Fig. 2F), and form with 6–8 tines more widely (30°) divergent (Fig. 2G); large uncinates (Fig. 2E) are of form typical of the family.

Microscleres: Oxyhexactins (Fig. 2H) to hemioxyhexasters (Fig. 2I) with smooth primary rays and micro-rough secondary rays numbering 1-4, often with branching retricted to one axis; discohexaster (or tylohexasters) with short smooth primary rays, each bearing 5 rough secondary rays terminating in a small cap with 4-6 marginal spines (Fig. 2J).

Remarks.—The specimen, SIO P 592, agrees in spiculation with that described by Koltun (1967) as *Aphrocallistes beatrix incognitus* (Table 1; Koltun 1967, Fig. 39). Koltun's material consisted of 2 small, damaged pieces of sponge, ca. 2.5 × 1.5 cm, plus numerous fragments of washed-out skeletal framework collected from the Okhotsk Sea. He was able to describe and measure dermal and parenchymal spicules but atrial surfaces were too damaged to enable determination of associated spicules critical to generic placement. Surprisingly he made no statements on framework structure or channelization, features which were available for assessment and critical for family assignment. His placement of the Okhotsk material was presumably influenced by the distinctive "roller-form" of the hemihexasters, a well known feature of *Aphrocallistes beatrix,* and compromised by the unavailability of atrial spicules and his lack of awareness of Ijima's *Heterochone.* With availability of the atrial surface in the southern California specimen, and conclusion that the specimen is conspecific with the Okhotsk material, Kotun's specimens can now be correctly reassigned as the new combination, *Heterochone incognitus* Koltun. The new form is easily differentiated from other *Heterochone* species: *H. calyx* Schulze has shorter inflated pinulus and spheric oxyhexasters; *H. hamata* Schulze has no oxyhexasters; *H. tenera* Schulze has microsclere populations that are mainly discohexactins.

Acknowledgments

I thank Spencer Luke and Larry Lovell for making loan material available for this study, and Prof. V.M. Kotun for providing holotype collection data. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada.

Literature Cited

Ijima, I. 1927. The Hexactinellida of the Siboga Expedition. Siboga Exped. Rept. 6:1–383.

Koltun, V.M. 1967. Vitreous sponges of the Northern and Far-Eastern Seas of the USSR. [in Russian] Opred. Faune S.S.S.R. 94:1–124.

Laubenfels, M.W. de 1932. Marine and fresh water sponges of California. Proc. U.S. Nat. Mus. 81: 1–140.

Reid, R.E.H. 1963. Notes on a classification of the Hexactinosa. J. Paleont. 37:218–231.

Reiswig, H.M. 1990. Correction of Ijima's (1927) list of recent hexactinellid sponges (Porifera). Proc. Biol. Soc. Wash. 103:731–745.

Schulze, F.E. 1886. Über den Bau und das System der Hexactinelliden. Abh. Königl. Akad. Wiss. Berlin (Physik.-Math.) 1886:1–97.

Accepted for publication 22 December 2000.

INSTRUCTIONS FOR AUTHORS

The BULLETIN is published three times each year (April, August, and December) and includes articles in English in any field of science with **an emphasis on the southern California area**. Manuscripts submitted for publication should contain results of original research, embrace sound principles of scientific investigation, and present data in a clear and concise manner. The current AIBS *Style Manual for Biological Journals* is recommended as a guide for contributors. Consult also recent issues of the BULLETIN.

MANUSCRIPT PREPARATION

The author should submit *at least two additional copies with the original,* on 8½ × 11 opaque, nonerasable paper, double spacing the entire manuscript. *Do not break words at right-hand margin anywhere in the manuscript.* Footnotes should be avoided. **Manuscripts which do not conform to the style of the BULLETIN will be returned to the author.**

An abstract summarizing in concise terms the methods, findings, and implications discussed in the paper *must* accompany a *feature article. Abstract should not exceed 100 words.*

A feature article comprises approximately five to thirty typewritten pages. Papers should usually be divided into the following sections: abstract, introduction, methods, results, discussion and conclusions, acknowledgments, literature cited, tables, figure legend page, and figures. Avoid using more than two levels of subheadings.

A research note is usually one to six typewritten pages and rarely utilizes subheadings. Consult a recent issue of the BULLETIN for the format of *notes.* Abstracts are not used for notes.

Abbreviations: Use of abbreviations and symbols can be determined by inspection of a recent issue of the BULLETIN. **Omit periods after standard abbreviations:** 1.2 mm, 2 km, 30 cm, but Figs. 1–2. Use numerals *before* units of measurements: 5 ml, but nine spines (10 or numbers above, such as 13 spines). The metric system of weights and measurements should be used wherever possible.

Taxonomic procedures: Authors are advised to adhere to the taxonomic procedures as outlined in the International Code of Botanical Nomenclature (Lawjouw et al. 1956), the International Code of Nomenclature of Bacteria and Viruses (Buchanan et al. 1958), and the International Code of Zoological Nomenclature (Ride et al. 1985). Special attention should be given to the description of new taxa, designation of holotype, etc. Reference to new taxa in titles and abstracts should be avoided.

The literature cited: Entries for books and articles should take these forms.

McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus.* J. Mamm., 54:452–458.

Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

Tables should not repeat data in figures *(line drawings, graphs, or black and white photographs) or contained in the text.* The author must provide numbers and short legends for tables and figures and place reference to each of them in the text. Each table with legend must be on a separate sheet of paper. All figure legends should be placed together on a separate sheet. **Illustrations and lettering thereon should be of sufficient size and clarity to permit reduction to standard page size;** *ordinarily they* **should not exceed 8½ by 11 inches** in size and after final reduction lettering must equal or exceed the size of the typeset. All half-tone illustrations will have light screen (grey) backgrounds. Special handling such as dropout half-tones, special screens, etc., must be requested by and will be charged to authors. As **changes may be required after review, the authors should retain the original figures in their files until acceptance of the manuscript for publication.**

Assemble the manuscript as follows: cover page (with title, authors' names and addresses), abstract, introduction, methods, results, discussion, acknowledgements, literature cited, appendices, tables, figure legends, and figures.

A cover illustration pertaining to an article in the issue or one of general scientific interest will be printed on the cover of each issue. Such illustrations along with a brief caption should be sent to the Editor for review.

PROCEDURE

All manuscripts should be submitted to the Editor, Daniel A. Guthrie, W. M. Keck Science Center, 925 North Mills Avenue, Claremont, CA 91711. **Authors are requested to submit the names, addresses and specialities of three persons who are capable of reviewing the manuscript. Evaluation of a paper** submitted to the BULLETIN begins with a critical reading by the Editor; several referees also check the paper for scientific content, originality, and clarity of presentation. Judgments as to the acceptability of the paper and suggestions for enhancing it are sent to the author at which time he or she may be requested to rework portions of the paper considering these recommendations. The paper then is resubmitted and may be re-evaluated before final acceptance.

Proof: The galley proof and manuscript, as well as reprint order blanks, will be sent to the author. He or she should **promptly** and **carefully read** the proof sheets for errors and omissions in text, tables, illustrations, legends, and bibliographical references. He or she marks corrections on the galley (copy editing and proof procedures in *Style Manual*) and **promptly returns both galley and manuscript** to the Editor. Manuscripts and original illustrations will not be returned unless requested at this time. **All changes in galley proof attributable to the author (misspellings, inconsistent abbreviations, deviations from style, etc.) will be charged to the author. Reprint orders are placed with the printer, not the *Editor.***

CONTENTS

A Fossil Blue Marlin (*Makaira nigricans* Lacépède) from the Middle Facies of the Trinidad Formation (Upper Miocene to Upper Pliocene), San José del Cabo Basin, Baja California Sur, México. Harry L. Fierstine, Shelton P. Applegate, Gerardo González-Barba, Tobias Schwennicke, and Luis Espinosa-Arrubarrena 59

Contributions to the Life History of Adult Pacific Lamprey (*Lampetra tridentata*) in the Santa Clara River of Southern California. Shawn D. Chase 74

Combined Effects of Drought and *Phoradendrom juniperinum* Infestation Severity on Fruit Characteristics of *P. juniperinum* and its *Juniperus osteosperma* Hosts. Simon A. Lei 86

Spatial Distribution of Blackbrush (*Coleogyne ramosissima* Torr.) Populations in the Mojave Desert. Simon A. Lei 96

Postfire Seed Bank and Soil Conditions in a Blackbrush (*Coleogyne ramosissima* Torr.) Shrubland. Simon A. Lei 100

Helminths of Six Species of Colubrid Snakes from Southern California. Stephen R. Goldberg and Charles R. Bursey 109

Helminths of the California Treefrog, *Hyla cadaverina* (Hylidae), from Southern California. Stephen R. Goldberg and Charles R. Bursey 117

A New North Pacific *Heterochone* Transferred from *Aphrocallistes* (Porifera: Hexactinellida). Henry M. Reiswig 123

COVER: *Makaira nigricans* Lacépède. Skull Lateral view (see Figure 1 in Fierstine, et al).

ISSN 0038-3872

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 100 **Number 3**

EL NIÑO SYMPOSIUM

BCAS-A100(3) 129–252 (2001) DECEMBER 2001

Southern California Academy of Sciences

Founded 6 November 1891, incorporated 17 May 1907

OFFICERS

Daniel Pondella, *President*
Ralph Appy, *Vice-President*
Susan E. Yoder, *Secretary*
Daniel A. Guthrie, *Treasurer*
Daniel A. Guthrie, *Editor*
David Huckaby, *Past President*
Hans Bozler, *Past President*

BOARD OF DIRECTORS

1999–2002	2000–2003	2001–2004
Ralph G. Appy	James Allen	Brad R. Blood
Jonathan N. Baskin	John Dorsey	Chuck Kopczak
John W. Roberts	Judith Lemus	Daniel Pondella
Tetsuo Otsuki	Martha and Richard Schwartz	Raymond Wells
Gloria J. Takahashi	Susan E. Yoder	Raymond Wilson

Membership is open to scholars in the fields of natural and social sciences, and to any person interested in the advancement of science. Dues for membership, changes of address, and requests for missing numbers lost in shipment should be addressed to: Southern California Academy of Sciences, the Natural History Museum of Los Angeles County, Exposition Park, Los Angeles, California 90007-4000.

Professional Members	$35.00
Student Members	20.00

Memberships in other categories are available on request.

Fellows: Elected by the Board of Directors for meritorious services.

The Bulletin is published three times each year by the Academy. Manuscripts for publication should be sent to the appropriate editor as explained in “Instructions for Authors” on the inside back cover of each number. All other communications should be addressed to the Southern California Academy of Sciences in care of the Natural History Museum of Los Angeles County, Exposition Park, Los Angeles, California 90007-4000.

Date of this issue 10 December 2001

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

QH1
.S69
v.100:3

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

CALL FOR PAPERS

2002 ANNUAL MEETING

June 7–8, 2002

CLAREMONT MCKENNA COLLEGE

CLAREMONT

Contributed Papers & Posters: Both professionals and students are welcome to submit abstracts for a paper or poster in any area of science. Abstracts are required for all papers, as well as posters, and must be submitted in the format described below. Maximum poster size is 32 by 40 inches.

Symposia: The following symposia are planned at the present time. If you wish to participate or to organize any additional symposia, please contact the organizer or the Academy Vice President, Ralph Appy (310 732 3497) rappy@portla.org. Organizers should have a list of participants and a plan for reaching the targeted audience.

Virtual Oceans
  Organizers: Judy Doino Lemus *jdlemus@usc.edu* 213-740-1965

Rocky Reef Monitoring
  Organizers: Dan Pondella *pondella@oxy.edu* (323) 259-2955 and Bob Grove *grovers@sce.com* 626-302-9735

Conservation Management
  Organizer: Brad Blood *BBlood@sapphosenvironmental.com* 626-683-3547

High School Science Education
  Organizers: Martha and Richard Schwartz *SCI1RS@aol.com*

SCCWRP Bight 98 Regional Monitoring
  Organizer: Stephen Wiesberg 714 372 9203 *stevew@sccwrp.org*

Effects of exotic species on Southern California wildlife
  Organizers: Dan Guthrie *dguthrie@jsd.claremont.edu* 909 607 2836 and Andrew Jirik *ajirik@portla.org*

Aerial Particulate Contaminants
  Ralph Appy *rappy@portla.org* 310-732-3497

CALIFORNIA
ACADEMY OF SCIENCES
DEC 26 2001
LIBRARY

There will be additional sessions of Invited Papers and Posters and of papers by Junior Academy members.

Student Awards: Students who elect to participate are eligible for best paper or poster awards in the following categories. Biology: ecology and evolution, biology: genetics and physiology, physical science. A paper by any combination of student and professional co-authors will be considered eligible provided that it represents work done principally by student(s). In the case of an award to a co-authored paper, the monetary award and a one year student membership to the Academy will be made to the first author only.

For further information on posters, abstracts, registration and deadlines, see the Southern California Academy of Science web page at: www.lam.mus.ca.us/~scas/

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 129–130

Proceedings of Special Symposium:

New and Rare Fish and Invertebrate Species to California during the 1997-1998 El Niño
Sponsored by
The Southern California Academy of Sciences
May 20, 2000

Daniel J. Pondella, II[1] and M. James Allen[2] Editors

[1]*Vantuna Research Group, Department of Biology, Moore Laboratory of Zoology, Occidental College, Los Angeles, California 90041*
[2]*Southern California Coastal Water Research Project, Westminster, California 92683*

Introduction

By some measures 1997–1998 El Niño southern oscillation (ENSO) was the strongest such event of the 20th century and perhaps the strongest of all recorded history. For most of us, an El Niño means increased rains in the Southern California area, due to a disruption of the normal path of the jet stream. In the study of marine ecology and fisheries biology, El Niño's have much more dire consequences. These winter storms can devastate our coastline and are accompanied by unusually warm and unproductive water. El Niño's have been cited as the cause of the collapse of fishery stocks as well as the demise of our world renowned kelp beds. ENSO events have increased in both frequency and magnitude for the past two decades, which has intensified our awareness of this global phenomenon. These changes, which we have seen in our coastal ecosystems, have implications of macroscale changes in oceanography extending far beyond the Southern California arena. As we sit on the precipice of the 21st century, the staggering ramifications of these new oceanographic conditions trigger questions of global climate change and we are challenged with the prospects of global warming.

The Southern California Bight, as a transitional zone between the cold temperate Oregonian fauna to the north and the warm subtropical San Diegan fauna to the south, is a critical oceanographic realm for studying the effects of such oceanographic disturbances. As our climate changes, our marine fauna responds rapidly within this region. It has been noted that organisms distributed to the south have the ability to migrate or colonize more northern locales during these anomalously warm periods. But, what is less well known is the long-term fate of these organisms. When our coastal waters cool, expatriated individuals may not survive. On the other hand, colonization during these warming events may result in permanent additions to our fauna, and a shift in the marine ecology of our region. The strength of the 1997–1998 ENSO was mirrored by an unusually high occurrence of subtropical organisms along the California coast. Considering that range extensions during ENSO events have reported for decades, it was our opinion that the whole new suite of organisms appearing during this period was of critical importance in aiding our understanding of the macroscale changes that may be occurring.

Part of the Southern California Academy of Science's mission is to disseminate information concerning scientific research in Southern California. We accomplish this primarily through two venues, our Annual Meeting and the Bulletin. On May 20, 2000 during our Annual Meeting at the University of Southern California we held a symposium entitled "New and Rare Fish and Invertebrate Species to California during the 1997–1998 El Niño." We drew on all aspects of our scientific community to compile the most complete synopsis of the effects of this event on the biology of macroinvertebrates and fishes. We are pleased that the participants of this symposium took the time out of their hectic schedules to compose the following papers and we hope that the following publication will heighten our awareness of the changes we are observing in our environment.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 131–136

First Occurrence of Blackspot Wrasse, *Decodon melasma* Gomon 1974 (Pisces: Labridae) in California

M. James Allen[1] and Ami K. Groce[2]

[1]*Southern California Coastal Water Research Project,*
Westminster, California, 92683
[2]*City of San Diego, Metropolitan Wastewater Department, Environmental*
Monitoring and Technical Services Division, San Diego, California 92106

Wrasses (family Labridae) are epibenthic, demersal, and water-column fishes found in coastal warm-temperate and tropical waters, usually near rocky and coral reefs of the Atlantic, Indian, and Pacific Oceans. Although this is the second largest family of marine fishes (Nelson 1994), only three species have been reported from California: rock wrasse, *Halichoeres semicinctus;* señorita, *Oxyjulis californica;* and California sheephead, *Semicossyphus pulcher* (Hubbs *et al.* 1979; Eschmeyer *et al.* 1983). This paper reports the first occurrences of a fourth species of wrasse in California.

Following the 1997–1998 El Niño, three specimens of a small labrid were collected in the Southern California Bight (SCB) by 7.6-m wide (headrope) semiballoon otter trawls with 1.2-cm cod-end mesh. The first specimen, 51 mm standard length (SL), was collected on 2 June 1998 off Dana Point, California (latitude 33°27.80′ N and longitude 117°44.85′ W) at a depth of 60 m. The second specimen (also 51 mm SL) was collected on 25 June, 1998 at a depth of 60 m off Laguna Beach, California (latitude 33°30.07′ N and longitude 117°49.40′ W). These fish were collected during a cooperative trawl survey between the Ocean Institute (Orange County Marine Institute at that time) and the Southern California Coastal Water Research Project (SCCWRP). Both specimens were identified at that time by M. J. Allen as the blackspot wrasse, *Decodon melasma* Gomon 1974. A third specimen (57 mm SL) was collected on 26 April, 1999 off San Diego, California (latitude 32°37.54′ N and longitude 117°19.37′ W) at a depth of 100 m. It was captured at one of the City of San Diego, Metropolitan Wastewater Department, Environmental Monitoring and Technical Services' long-term, fixed-location trawl monitoring stations. City of San Diego marine biologists brought this specimen to the attention of R. H. Rosenblatt (Scripps Institution of Oceanography; SIO), who identified it as *Decodon melasma.* All three specimens have been catalogued in the SIO Marine Vertebrates Collection: SIO 99-100 (San Diego); SIO 00-77 (Dana Point); and SIO 00-78 (Laguna Beach).

The capture of blackspot wrasse at Laguna Beach, CA represents a range extension of more than 1,500 km north of its northernmost record (Gomon 1974). The three specimens are the first records of the species outside of the Gulf of California north of Cabo San Lucas (latitude 22°45′ N). Based on the new specimens, the current geographic range of black spot wrasse is now from Laguna Beach, California and the northern Gulf of California to Peru, including Cocos Islands (Gomon 1974; Allen and Robertson 1994). Its range extends along the warm-temperate San Diego and Cortez Provinces and the tropical Mexican and

Table 1. Location and meristic data for blackspot wrasse, *Decodon melasma* specimens collected in southern California in 1998 and 1999.

	Specimens		
Category	SIO 00-77	SIO 00-78	SIO 99-100
Collection information			
Date	2 Jun 98	25 Jun 98	26 Apr 99
Location	Dana Point, CA	Laguna Beach, CA	San Diego, CA
Latitude N	33°27.80′	33°30.07′	32°37.54′
Longitude W	117°44.85′	117°49.40′	117°19.37′
Depth (m)	60	60	100
Standard Length (mm)	51	51	57
Meristic Counts			
Dorsal Fin Elements	X, 10	XII, 9	XI, 10
Anal Fin Elements	III, 10	III, 10	III, 10
Pectoral Fin Rays	17	17	16
Pelvic Fin Elements	I, 5	I, 5	I, 5
Lateral line pores	29	29	Scales missing
Gill Rakers	5 + 9 = 14	5 + 9 = 14	5 + 9 = 14

Panamic Provinces of Briggs (1974). Blackspot wrasse occurs on flat sandy to soft bottoms, often with some rocky rubble or patch reefs at depths of 40 to 160 m (Gomon 1974), and as such, is characteristic of the middle and outer shelf zones of Allen and Smith (1988). It occurs in deeper water and on a different habitat (soft-bottom) than the other California species, which are inner shelf (<30 m) rocky bottom and kelp bed species (Feder *et al.* 1974).

The three California specimens had similar meristics (Table 1) and color patterns. They had five dusky bars on the back (about two to three scales in width), extending ventrally from the dorsal fin, across the lateral line, and to the midlateral body, fading ventrally, with a dark spot on each side of the dorsal caudal peduncle (Fig. 1). The color of the body was similar to that shown in Allen and Robertson (1994). The body was pink, fading to white on the abdomen, on the pectoral fin base, and under the pelvic fins. The nape, top of head, and snout were dusky, with white on the head below the eye, and on the lower jaw. The head posterior to the eye was pink extending from there to the dorsal base of the pectoral fin. The upper lip was yellow posteriorly, around the anterior and ventral rim of the

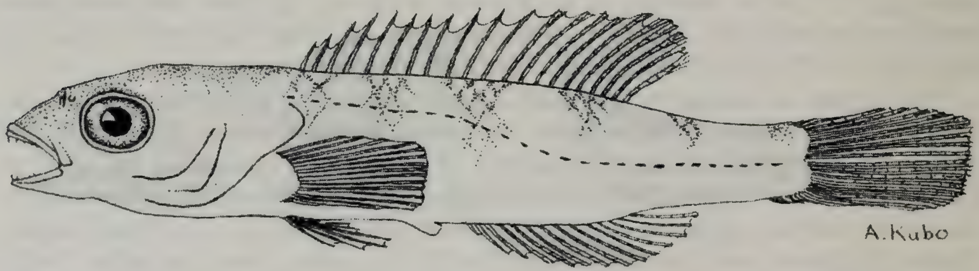


Fig. 1. Juvenile (51 mm standard length) blackspot wrasse, *Decodon melasma,* collected off Laguna Beach, California, at depth of 60 m on June 25, 1998; SIO 00-78 (drawing by Atsuhiro Kubo).

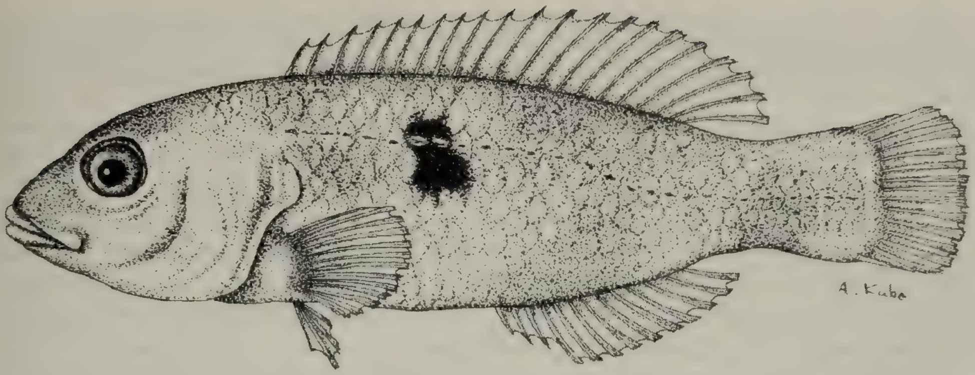


Fig. 2. Adult (140 mm standard length) blackspot wrasse, *Decodon melasma* (drawing by Atsuhiro Kubo, based on photograph in Gomon 1974).

eye was yellow, and a yellow line extended posteroventrally from the eye onto the operculum. There was a yellow spot on the posterior operculum dorsal to this line, and the preopercular area was yellow. The spinous dorsal fin was dusky on the dorsal edge, with a black spot on dorsal spines 11 to 13. The anal fin was yellowish with a white edge, the caudal fin and pelvic fins white, and the pectoral fin pink. The eyes had black edges dorsally, fading to yellow, then red around most of the pupil.

The blackspot wrasse has a relatively elongate compressed body (depth 20–32% of standard length, increasing with size) (Figs. 1 and 2) (Gomon 1974, 1995). Adults (not yet observed in California) have relatively blunt heads, slightly subterminal mouths (Fig. 2). The body is red dorsally and white below, with head red dorsally, white ventrally, and with three yellow stripes below the eye. Merisitic elements have the following ranges (from Gomon 1974, Watson 1996, and new California specimens): dorsal fin (X-XII,9–10); anal fin (III,9–10); pectoral fin (14–18); pelvic fins (I,5); branchiostegal rays (6); lateral line scales and pores (28–29); and gill rakers (5−7+9−12=14−19). It has caniniform teeth, with two pairs at the anterior of each jaw enlarged (Gomon 1974, Allen and Robertson 1994).

Characters that distinguish blackspot wrasse from other California labrids are the following: 1) scaly head with lower limb of preopercle scaly; 2) large scales (28–29 in lateral line); 3) 10–12 dorsal spines; 4) adult coloration—red with a black spot dorsolateral on body and yellow eye stripes; and 5) juvenile coloration—pinkish red with up to 6 dusky bars above the lateral line, yellow eye stripes, and a dark spot on the spinous dorsal fin (Table 2). Blackspot wrasse is more similar in characteristics to California sheephead than to rock wrasse or señorita. Maximum size of adult blackspot wrasse is 23 cm in length (Gomon 1995).

Blackspot wrasse first occurred in California during the 1997–1998 El Niño period, as did several other species (Lea and Rosenblatt 2000). It is likely that its larvae came into the Southern California Bight with the warm water mass from the south. It is not known if these individuals are the result of long-distance dispersal from a distant population (1,500 km away) or whether they dispersed from populations along the outer coast of Baja California, which is less well sampled. Many shallow-living wrasses transform at a small size (Watson 1996)

Table 2. A key to species and life stages of wrasses, family Labridae, of California. Based on information in Jordan and Evermann (1898), Miller and Lea (1972), Gomon (1974), Eschmeyer *et al.* (1983), Allen and Robertson (1994), Nelson (1994), Gomon (1995), Humann (1996), and Watson (1996).

Characteristics of California Labridae: Mouth protractile; jaw teeth separate, projecting outward; dorsal fin with 8–14 spines and 9–13 soft rays; anal fin with 3 spines and 9–13 soft rays; caudal fin with 7+7 principal caudal rays; pectoral rays 12–19 soft rays; pelvic fins, 1 spine and 5 soft rays; 6 branchiostegal rays; gill rakers, 5–8 (upper limb) + 9–16 (lower limb) (note, gill raker counts for *Semicossyphus pulcher* are 6–7 + 10–11 = 17–19; R. N. Lea, Calif. Dep. Fish Game, pers. comm.); lateral line scales, 26 to 60; lateral line continuous.

1a. Dorsal spines 10–12; sides of head more or less scaly; pink or red coloration on body 2

1b. Dorsal spines 8 to 10; head mostly naked; body color yellow to brown (sometimes green) 3

2a. Scales large (28 to 29 in lateral line); lower limb of preopercle scaly; one or more dark blotches dorsolaterally on sides; yellow eye stripes. . . . . . .blackspot wrasse, *Decodon melasma*

- a. Single dark spot dorsolaterally on side (Fig. 2); body depth 25–30%; color red; >13 cm SL. . . . . adult
- b. Five to six dark bars on back (one on dorsal caudal peduncle) (Fig. 1); body depth about 20–25% of standard length; color pink; <13 cm SL . . . . juvenile

2b. Scales small (about 60 in lateral line); lower limb of preopercle naked. . . . . California sheephead, *Semicossphus pulcher*

- a. Head and tail black, midbody red, chin white; body deep, compressed; >30 cm SL . . . . terminal phase (male)
- b. Fins without spots; body deep, compressed, pinkish with white chin; length 15 to 30 cm SL . . . . .initial phase (female)
- c. Single white stripe on side; black spots on anterior and posterior dorsal fin, dorsolateral caudal base, anal fin, and pelvic fins; body deep, reddish; <15 cm SL . . . . juvenile.

3a. Posterior canines well developed on both sides; dorsal spines pungent . . . . rock wrasse, *Halichoeres semicinctus*

- a. Body with black bar behind pectoral fin, back unmarked or with multiple bars; >30 cm SL. . . . . terminal phase (male)
- b. Black flecks generally present on body; length 12 to 30 cm SL. . . . . .initial phase (female)
- c. Body with two white stripes on side of body, and two black spots on dorsal fin; body elongate compressed; yellow, orange, or green; <12 cm SL . . . . juvenile

3b. Posterior canines rudimentary; dorsal spines slender, very flexible señorita, *Oxyjulis californica*

- a. Body with broad black spot on the caudal fin at base of fin; >2.5 cm SL. . . . . .juvenile and adult
- b. Body with a black spot on posterior dorsal and anal fins; length less 2.5 cm. . . . . .small juvenile

---

and may be planktonic as eggs and larvae for about a month. Blackspot wrasse (a deeper-living species) may transform at a larger size (as do many deeper living species of other families; Moser 1996). If so, they may spend more time in the plankton (perhaps to 3 mo), and travel further in the current before settling. Assuming current velocities of 2 to 10 cm/sec without eddies (based on extreme values for the California Current; Hickey 1993), eggs and larvae could travel about 50–250 km in one month or 150–800 km in three months in a north flowing current. Given that both of these distances fall short of the 1,500 km distance from Cabo San Lucas, it is likely that the individuals captured in June 1998 in California came from spawning populations off the coast of northern Baja California. However, the individual caught in January 1999 (after the El Niño had subsided) may have been spawned off either southern California or northern Baja California. The generally tropical distribution of the species and the warm-temperate or cooler environment of the outer coast of Baja California suggests that the species may have expanded northward along the Baja California coast during the ocean warming of the past two decades (Smith 1995).

Thus it is likely that the blackspot wrasse had spawning individuals in or near southern California and was spawning during this period. The two fish captured in June 1998 (both 51 mm) were probably spawned in spring of 1998 while the one captured in January 1999 (57 mm) was probably spawned in fall or early winter of 1998. Blackspot wrasse may spawn from spring through fall as do the other California labrids (Watson 1996). Adults of the blackspot wrasse appear to be synchronous hermaphrodites in all but very large individuals (Gomon 1974). Individuals with two well-developed ovaries and a small testis on the left side occur at least to 150 mm SL; individuals with just testicular tissue occur from 138 to 200 mm SL (Gomon 1974).

Little is known about the ecology or behavior of this species. However, its general body morphology as an adult (i.e., elongate compressed, slightly inferior mouth, caniniform teeth) and behavior of morphologically similar labrids (Hobson 1968) suggests that it may be a solitary species that cruises over the bottom while foraging on small benthic crustaceans. Blackspot wrasse is a geminate species of the red hogfish, *Decodon puellaris,* of the Atlantic, which occupies similar depths (6–275 m) and habitat on the Atlantic and Caribbean between South Carolina and northeastern Brazil, and which grows to a similar size (15 cm) (Gomon 1974; Robins *et al.* 1986).

The common name 'blackspot wrasse' was suggested by its scientific name *melasma* (black spot) in reference to the black dorsolateral spot on each side of the body (Gomon 1974). This name has been used in Allen and Robertson (1994), Gomon (1995), and Escobar-Fernandez and Siri (1997). Bussing and Lopez (1994) used 'blotched hogfish.' As this species has not yet been included in the American Fisheries Society Checklist of Common and Scientific Names of Fishes of the United States and Canada (see Robins *et al.* 1991), we recommend the common name "blackspot wrasse" as the English common name for this species. In Spanish, this species has been called "lorito marcado" (Bussing and Lopez 1994) and "señorita de mancha negra" (Gomon 1995, Escobar-Fernandez and Siri 1997).

Acknowledgments

The authors thank the crew members of the Orange County Marine Institute (now Ocean Institute), particularly Julie Goodson (now at Channel Islands National Marine Sanctuary) and Shelly Moore (Southern California Coastal Water Research Project) for recognizing the first two specimens as different and submitting them for identification. We also thank the crew of the City of San Diego Ocean Monitoring Program (especially Steven Lagos) for recognizing the third specimen as different. We thank Atsuhiro Kubo for providing the drawings of the Laguna Beach specimen and of an adult. We also thank Phillip Hastings and H. J. Walker of Scripps Institution of Oceanography, University of California, San Diego and Richard Feeney and Jeffrey Siegel of the Natural History Museum of Los Angeles for collection information on blackspot wrasse.

Literature Cited

Allen, G. R., and D. R. Robertson. 1994. Fishes of the tropical eastern Pacific. University of Hawaii Press, xix + 332 pp.

Allen, M. J., and G. B. Smith. 1988. Atlas and zoogeography of common fishes in the Bering Sea and northeastern Pacific. NOAA Tech. Rep. NMFS 66. iii + 151 pp.

Briggs, J. C. 1974. Marine zoogeography. McGraw-Hill Book Co., 457 pp.

Bussing, W. A., and M. I. Lopez. 1994 (1993 on back cover but printed in Feb 1994). Demersal and pelagic inshore fishes of the Pacific coast of lower central America. Rev. Biol. Trop., Spec. Publ., 164 pp.

Eschmeyer, W. N., E. S. Herald, and H. Hammann. 1983. A field guide to Pacific Coast fishes of North America. Houghton Mifflin Company, xii + 336 pp.

Escobar-Fernández, R., and M. Siri. 1997. Nombres vernáculos y científicos de los peces del Pacífico mexicano. [Vernacular and scientific names of fishes of the Mexican Pacific]. Universidad Autónoma de Baja California, Sociedad Ictiológica Mexicana, A. C., MX, 102 pp.

Feder, H. M., C. H. Turner, and C. Limbaugh. 1974. Observations on fishes associated with kelp beds in southern California. Calif. Dep. Fish Game, Fish Bull. 160. 138 pp.

Gomon, M. F. 1974. A new Eastern Pacific labrid (Pisces), *Decodon melasma,* a geminate species of the western Atlantic *D. puellaris.* Proc. Biol. Soc. Wash. 87(54):621–629.

Gomon, M. F. 1995. Labridae. Pp. 1201-1225 *in* Guía FAO para la identificacíon de especies para los fines de la pesca. Pacífico centro-oriental. Vol. III. Vertebrados—Parte 2. (W. Fischer, W. Schneider, C. Sommer, K. E. Carpenter, and V. H. Niem, eds.), United Nations, Food and Agriculture Administration, xiii + 1,813 pp.

Hickey, B. M. 1993. Physical oceanography. Pp. 19-70 *in* Ecology of the Southern California Bight. (M. D. Dailey, D. J. Reish, and J. W. Anderson, eds.), Univ. Calif. Press, xvi + 926 pp.

Hobson, E. S. 1968. Predator behavior of some shore fishes in the Gulf of California. U. S. Dep. Interior, Fish Wildl. Serv., Bur. Sport Fish. Wildl., Washington, DC. Res. Rep. 73, vi + 92 pp.

Hubbs, C. L., W. I. Follett, and L. J. Dempster. 1979. List of fishes of California. Occas. Pap. Calif. Acad. Sci. 133. 51 pp.

Humann, P. 1996. Coastal fish identification: California to Alaska. New World Publications, Inc., 210 pp.

Jordan, D. S., and B. W. Evermann. 1898. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the isthmus of Panama. Part II. Bull. U. S. Natl. Mus. No. 47: 1241–2183.

Lea, R. N., and R. H. Rosenblatt. 2000. Observations on fishes associated with the 1997-1998 El Niño of California. Calif. Coop. Oceanic Fish. Inves. Rep. 41: 117–129.

Miller, D. J., and R. N. Lea. 1972 (addendum added 1976). Guide to coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157. 249 pp.

Moser, H. G. (ed.), The early stages of fishes in the California Current Region. Coop. Fish. Invest. Atlas No. 33. Allen Press Inc., Lawrence, KS. xii + 1505 pp.

Nelson, J. S. 1994. Fishes of the world. Third edition. John Wiley & Sons, Inc., xvii + 600 pp.

Robins, C.R., R.M. Bailey, C.E. Bond, J.R. Brooker, E.A. Lachner, R.N. Lea, and W.B. Scott. 1991. Common and scientific names of fishes from the United States and Canada. 5th edition. American Fisheries Society Special Publications 20. 183 pp.

Robins, C. R., G. C. Ray, J. Douglass, and R. Freund. 1986. A field guide to Atlantic Coast fishes of North America. Houghton Mifflin Company, xi + 354 pp.

Smith, P.E. 1995. A warm decade in the Southern California Bight. California Cooperative Oceanic Fisheries Investigations Reports 36: 120–126.

Watson, W. 1996. Labridae: Wrasses. Pp. 1088–1103 *in* The early stages of fishes in the California Current Region. (H. G. Moser, ed.), Coop. Fish. Invest. Atlas No. 33. Allen Press Inc., xii + 1505 pp.

Accepted for publication 21 December 2000.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 137–143

First Occurrence of Speckletail Flounder, *Engyophrys sanctilaurentii* Jordan & Bollman 1890 (Pisces: Bothidae), in California

M. James Allen[1] and Ami K. Groce[2]

[1]*Southern California Coastal Water Research Project, Westminster, California, 92683*
[2]*City of San Diego, Metropolitan Wastewater Department, Environmental Monitoring and Technical Services Division, San Diego, California 92106*

Currently there are 29 species of flatfishes representing three families (Paralichthyidae, Pleuronectidae, and Cynoglossidae) in California, with an additional species and family (Pacific lined sole, *Achirus mazatlanus;* family Achiridae) reported just below the United States-Mexico International Border (Hubbs *et al.* 1979; Lea *et al.* 1989; Lea, in prep.). This paper reports the first occurrence of the 30th species of flatfish in California and the first occurrence of the family Bothidae in the state. Seven California species (gulf sanddab, *Citharichthys fragilis;* Pacific sanddab, *Citharichthys sordidus;* speckled sanddab, *Citharichthys stigmaeus;* longfin sanddab, *Citharichthys xanthostigma;* bigmouth sole, *Hippoglossina stomata;* California halibut, *Paralichthys californicus;* and fantail sole, *Xystreurys liolepis*) placed in Bothidae in Robins *et al.* (1991) and earlier references have been placed in Paralichthyidae by most recent authoritative references (Nelson 1994, Hensley 1995b, Moser and Sumida 1996, Eschmeyer 1998).

On August 6, 1998, an unusual flatfish, 80 mm standard length (SL), was collected north of La Jolla Submarine Canyon, California (latitude 32°53.32′ N and longitude 117°16.66′ W) at a depth of 63 m in a 7.6-m wide (headrope) semiballoon otter trawl with 1.2-cm cod-end mesh. It was collected during the Southern California Bight 1998 Regional Survey (Bight'98), a bight-wide survey of the mainland and island shelves of southern California coordinated by the Southern California Coastal Water Research Project. Scientists working for the City of San Diego, Metropolitan Wastewater Department, Environmental Monitoring and Technical Services brought the specimen to the attention of M. J. Allen, who identified it as a speckletail flounder, *Engyophrys sanctilaurentii* Jordan & Bollman 1890. This specimen has been catalogued in the Scripps Institution of Oceanography (SIO) Marine Vertebrates Collection (SIO 00-81).

Although the speckletail flounder occurs commonly along the southern coast of Mexico, Central America, and northwestern South America, it had not previously been caught north of Sebastian Vizcaino Bay, Baja California, Mexico (Moser and Charter 1996). The capture of the speckletail flounder off La Jolla, California represents a range extension of 600 km north of its northernmost record (published and unpublished) and the first record of this species in California. Based on this specimen, the current geographic range of speckletail flounder is now from La Jolla, California and the northern Gulf of California (SIO 60-120: latitude 30°22.3′N, longitude 113°08.0′W) to Peru (Hensley 1995a). Its range extends along the warm-temperate San Diego and Cortez Provinces and the tropical Mexican and Panamic Provinces of Briggs (1974). Speckletail flounder occurs on mud, sand, gravel, or shell bottoms at depths of 10 m (LACM 32559.004) to 232 m (Hensley 1995a), with most specimens deeper than 40 m, and is thus characteristic of the middle and outer shelf zones of Allen and Smith (1988).

The specimen has the following characteristics (Fig. 1): left-eyed; small mouth reaching to the anterior part of the eye; teeth only on the blind side; narrow interorbital ridge between eyes with a small sharp spine facing posteriorly; dorsal fin beginning slightly on blind side of head behind posterior nostril; pectoral fins relatively short; pelvic fins short, asymmetrical with the left having longer base and on ventral midline about two rays anterior to the right fin on blind side; rounded caudal fin; high arch in lateral line over the pectoral fin and a short anterior bifurcating branch; no lateral line on the blind side. The specimen has the following meristic characteristics: dorsal fin rays—81; anal fin rays—67; pectoral rays—11; pelvic fin rays—6; lateral line pores, eyed side—65; and lateral line pores, blind side—0. Body scales ctenoid and imbricating. Gill membranes entirely separate. The coloration olive tan on the eyed side with dark spots on the body and medial fins: five along each margin of body near dorsal and anal fins; three along lateral line posterior to arch; six each on dorsal and anal fins; and posterior edge of caudal fin with four dark blotches (Fig. 1). The blind side dusky posteriorly and white anteriorly with five curved, dusky bands on anterior body and head. The anteriormost extends upward and backward from the cheek to dorsal margin of body, the next arches upward and backward from preopercle, the third arches backward from the opercle, the fourth (broken) arches upward and backward from the ventral body margin below the pectoral fin; and the fifth almost defines a circle behind the gut cavity.

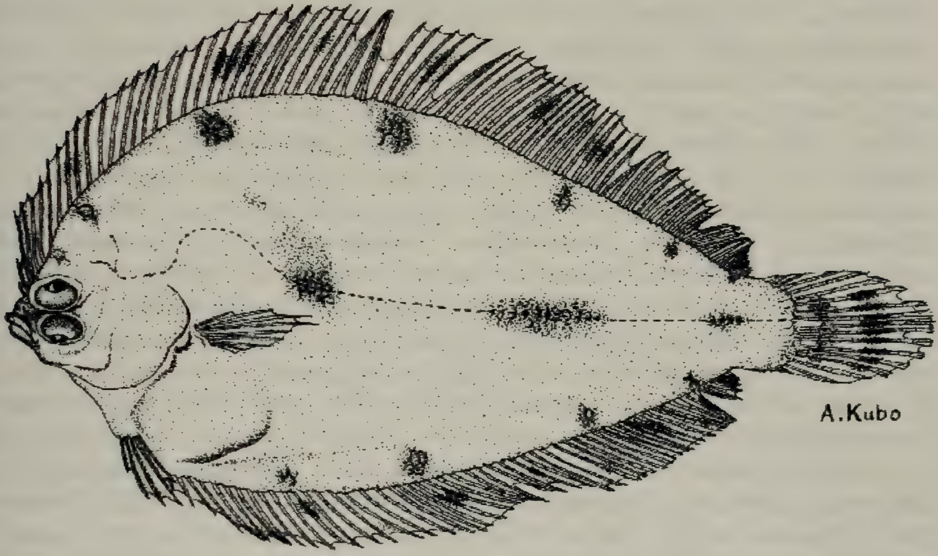
Combining this information with that in the literature (Jordan and Evermann 1898; Norman 1934; Hensley 1995a; Moser and Charter 1996), speckletail flounder has the following ranges of meristics: dorsal fin (78–89); anal fin (66–72); pectoral fins (10–13); pelvic fins (6); caudal fin (17 total); gill rakers (3–4 upper, 6 lower); lateral line pores (64–68 eyed side, no lateral line on blind side); lateral line scales (59–68). Its maximum reported size is 200 mm total length (Hensley 1995a).

Speckletail flounder is the only California flatfish with the following characters in combination: left-eyed; small mouth (reaching anterior part of eye); jaw teeth only on the blind side; a narrow interorbital crest between the eye with a backward facing spine; dorsal and anal fins separate from caudal fin; rounded caudal fin with four to five dark blotches; five to six curved dusky bands on blind side of body; lateral line of eyed side with high arch over the pectoral fin and a short bifurcating branch anteriorly, and no lateral line on blind side; and asymmetrical pelvic fins with that of eyed side on ventral midline, having longer base, and beginning two rays more anteriorly than that of blind side. The curved dusky

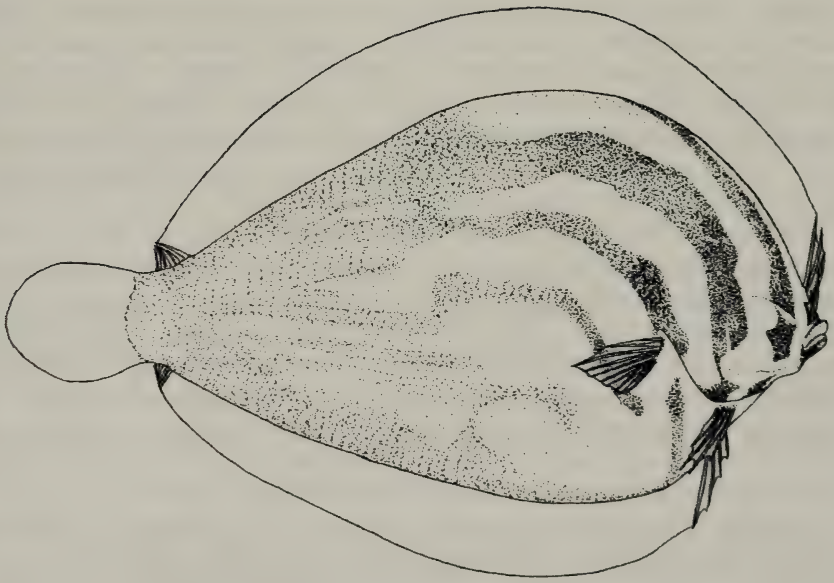
→

Fig. 1. Speckletail flounder, *Engyophrys sanctilaurentii,* (80 mm SL) collected near La Jolla Canyon, California at a depth of 63 m on August 6, 1998 (SIO 00-81): a) Eyed side (scale patches indicate size of scales on body); and b) blind side (details of medial fin rays are not shown). Drawings by Atsuhiro Kubo.

a)



b)



bands on the blind side are faint or obsolete in small individuals (Jordan and Evermann 1898) and sometimes fade in larger individuals with preservation.

This species was one of a number of species collected for the first time in California or the Southern California Bight during the 1997–1998 El Niño (Lea and Rosenblatt 2000). Speckletail flounder transforms at a length of 27–37 mm, a size typical of flatfish species spending a longer time in the plankton and settling on the middle or outer shelf habitats (Richardson and Pearcy 1977; Allen 1982; Kramer 1991; Charter and Moser 1996; Moser and Charter 1996; Moser and Sumida 1996). For comparison, eggs and larvae of California halibut are in the plankton for about one month before settling to the bottom in shallow water at 10 mm SL (Allen 1988). As speckletail flounder transforms at a larger size, it may be in the plankton for a longer period (perhaps to about three months). If so, the species could reach southern California from Sebastian Vizcaino Bay (about 600 km distance) during this period if water currents were about 7.5 cm/sec, without eddies. Extreme values for the California Current range from 2 to 10 cm/sec (Hickey 1993). Thus it is possible that speckletail flounder spawned near its reported northern limit could reach southern California during this period. It is probably more likely the specimen collected was transported north from spawning in unreported populations further north along the Baja California coast than its reported range. The generally tropical distribution of the species and the warm-temperate or cooler environment of the outer coast of Baja California suggests that the species may have expanded northward along the Baja California coast during the ocean warming of the past two decades (Smith 1995).

Speckletail flounder larvae can be taken year-round (Moser and Charter 1996). The age of the specimen collected is not known. If the 80 mm SL specimen collected in southern California represents young of the year, it may have been spawned in fall of 1998, settling in southern California between fall and early spring during the middle of the El Niño. If it is older, then its occurrence in southern California cannot be attributed to the 1997–1998 El Niño.

Little is known about the ecology or behavior of this species. However, the general body morphology as an adult (i.e., small mouth with teeth only on blind side, sharp ridge between the eyes) is quite similar to that of pleuronectid flatfishes of the genus *Pleuronichthys,* (Allen 1982). Given its depth range, this species may be an ecological counterpart of the hornyhead turbot, *Pleuronichthys verticalis,* which occurs off California and the outer coast of Baja California and of the ocellated turbot, *Pleuronichthys ocellatus,* which occurs in the northern Gulf of California (Fitch 1963, Allen 1982). At least among southern California flatfishes, the absence of teeth on the eyed-side of the jaws is characteristic of flatfishes that extract polychaetes from tubes and clip off clam siphons (Allen 1982). Other species of small-mouthed flatfishes with jaw teeth only on blind side apparently do not occur along the coast of Mexico south of Baja California nor off Central America (Norman 1934; Hensley 1995a,b; Sommer 1995). There are, however, several species of paralichthyids which have reduced tooth development on jaws on the eyed side (Norman 1934; Hensley 1995b), a morphology that is somewhat less appropriate for this type of foraging behavior (Allen 1982).

There are a number of nomenclatural problems associated with the names (both scientific and common) of this species. The genus and species was first described by Jordan and Bollman (1890). The date of 1889 originally given for this citation

(Jordan and Evermann 1898) is incorrect as the signature date of this document was February 5, 1890 (Hays 1952). The original species name was *sancti-laurentii,* named for Saint Lawrence, and referring to the gridiron-like markings on the blind side. Since that time, the name has been variously given in the literature as *sancti-laurentii* (Jordan and Bollman 1890; Jordan and Evermann 1898; Norman 1934), *sanctilaurentii* (Bussing and Lopez 1994; Eschmeyer 1998), or *sanctilaurentia* (Hensley 1995a; Moser and Charter 1996; Escobar-Fernandez and Siri 1997). The International Code of Zoological Nomenclature (ICZN 1999) indicates that hyphens should be removed from compound species-group names originally published with a hyphen (unless the first element is a Latin letter) and both words should be united. Thus the hyphenated version is not appropriate. Regarding the correct ending, 'ii' is used if the name refers to a male person and 'ia' if it refers to a quality, state of being, or disease (Jaeger 1966). The species was named after Saint Lawrence, a 3rd century AD deacon of the early Catholic church who was tortured to death by a Roman prefect on a hot grill, which branded him with gridiron marks (Kirsch 1910). Thus, 'ia' would refer to the condition of having the gridiron marks similar to those of Saint Lawrence whereas 'ii' would refer to Saint Lawrence, the person who had the gridiron marks. Although Jordan and Bollman (1890) refer to the gridiron pattern on the fish for justifying the name, the name they gave was of the person rather than the Latinized version of the grid-iron condition. Hence, it appears appropriate to maintain the original ending of the name, with the correct species name (without a hyphen) for this species being *sanctilaurentii.*

Published English common names for this species include 'speckletail flounder' (Bussing and Lopez 1994); 'speckled-tail flounder' (Hensley 1995a), and 'speckledtail flounder' (Escobar-Martinez and Siri 1997). The American Fisheries Society Committee on Names of Fishes (Robins *et al.* 1991) recommends that common names be simple and with no hyphens, unless it is necessary to avoid misunderstanding. Although there is precedent for combining plural modifiers with nouns to form compound modifying words (e.g., 'spottedtail goosefish', 'spottedfin tonguefish', and 'stripedfin ronquil') in Robins *et al.* (1991), there is no precedent for 'speckledtail.' 'Speckle' when combined with a noun is always treated as singular (e.g., 'specklefin midshipman', 'specklemouth eelpout'), presumably due to the generally plural nature of 'speckle.' Thus we recommend 'speckletail flounder' as the common name for this species.

Acknowledgments

The authors thank Steven Lagos of the City of San Diego Ocean Monitoring Program for retaining the specimen for further identification. We thank Atsuhiro Kubo for providing drawings of the La Jolla specimen. We also thank Phillip Hastings and H. J. Walker of Scripps Institution of Oceanography, University of California, San Diego and Richard Feeney and Jeffrey Siegel of the Natural History Museum of Los Angeles for collection information on speckletail flounder.

Literature Cited

Allen, L. G. 1988. Recruitment, distribution, and feeding habits of young-of-the-year California halibut (*Paralichthys californicus*) in the vicinity of Alamitos Bay-Long Beach Harbor, California, 1983–1985. Bull. So. Calif. Acad. Sci. 87(1):19–30.

Allen, M. J. 1982. Functional structure of soft-bottom fish communities of the southern California shelf. Ph.D. dissertation. University of California, San Diego, xxvi + 577 pp.

Allen, M. J., and G. B. Smith. 1988. Atlas and zoogeography of common fishes in the Bering Sea and northeastern Pacific. NOAA Tech. Rep. NMFS 66. 151 pp.

Briggs, J. C. 1974. Marine zoogeography. McGraw-Hill Book Co., 457 pp.

Bussing, W. A., and M. I. Lopez. 1994 (1993 on back cover but printed in Feb 1994). Demersal and pelagic inshore fishes of the Pacific coast of lower central America. Rev. Biol. Trop., Spec. Publ., 164 pp.

Charter, S. R., and H. G. Moser. 1996. Pleuronectidae: righteye flounders. Pp. 1369–1403 *in* The early stages of fishes in the California Current Region. (H. G. Moser, ed.), Coop. Fish. Invest. Atlas No. 33. Allen Press Inc., xii + 1505 pp.

Eschmeyer, W. N. (ed.) 1998. Catalog of fishes. Calif. Acad. Sci, San Francisco, CA. 2905 pp.

Escobar-Fernández, R., and M. Siri. 1997. Nombres vernáculos y científicos de los peces del Pacífico mexicano. [Vernacular and scientific names of fishes of the Mexican Pacific]. Universidad Autónoma de Baja California, Sociedad Ictiológica Mexicana, A. C., MX. 102 pp.

Fitch, J. E. 1963. A review of the genus *Pleuronichthys.* Los Angeles County Museum, Los Angeles, California. Contrib. in Sci. 76. 33 pp.

Hays, A. N. 1952. David Starr Jordan: a bibliography of his writings, 1871–1931. Stanford Univ. Press, Stanford, CA. 195 pp.

Hensley, D. A. 1995a. Bothidae. Pp. 931–936 *in* Guía FAO para la identificacíon de especies para los fines de la pesca. Pacífico centro-oriental. Vol. II. Vertebrados—Parte 1, (W. Fischer, W. Schneider, C. Sommer, K. E. Carpenter, and V. H. Niem, eds.), United Nations, Food and Agriculture Administration, xiii + 1,813.

Hensley, D. A. 1995b. Paralichthyidae. Pp. 1349–1380 *in* Guía FAO para la identificacíon de especies para los fines de la pesca. Pacífico centro-oriental. Vol. III. Vertebrados—Parte 2, (W. Fischer, W. Schneider, C. Sommer, K. E. Carpenter, and V. H. Niem, eds.), United Nations, Food and Agriculture Administration, xiii + 1,813.

Hickey, B. M. 1993. Physical oceanography. Pp. 19–70 *in* Ecology of the Southern California Bight. (M. D. Dailey, D. J. Reish, and J. W. Anderson, eds.), Univ. Calif. Press, xvi + 926 pp.

Hubbs, C. L., W. I. Follett, and L. J. Dempster. 1979. List of fishes of California. Occas. Pap. Calif. Acad. Sci. 133. 51 pp.

ICZN (International Commission on Zoological Nomenclature). 1999. International code of zoological nomenclature. Fourth edition. International Trust for Zoological Nomenclature, xxix + 306 pp.

Jaeger, E. C. 1966. A source-book of biological names and terms. Third edition. Charles C. Thomas, Publisher, xxxv + 323 pp.

Jordan, D. S., and C. H. Bollman. 1890. Descriptions of new species of fishes collected at the Galápagos Islands and along the coast of the United States of Colombia, 1887–88. Proc. U. S. Natl. Mus. 12(770):149–183.

Jordan, D. S., and B. W. Evermann. 1898. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America north of the Isthmus of Panama. Part III. Bull. U. S. Natl. Mus. No. 47:2183–3136.

Kirsch, J. P. 1910. St. Lawrence. *In* The Catholic Encyclopedia, Vol. IX. Robert Appleton Company.

Kramer, S. H. 1991. Growth, mortality, and movements of juvenile California halibut *Paralichthys californicus* in shallow coastal and bay habitats of San Diego, California. Fish. Bull. (U.S.) 89: 195–207.

Lea, R. N., K. A. Karpov, and L. F. Quirillo. 1989. Record of the roughscale sole, *Clidoderma asperrimum,* from northern California, with a note on the Pacific lined sole, *Achirus mazatlanus.* Calif. Fish Game 75(4):239–241.

Lea, R. N., and R. H. Rosenblatt. 2000. Observations on fishes associated with the 1997–1998 El Niño of California. Calif. Coop. Oceanic Fish. Inves. Rep. 41: 117–129.

Moser, H. G., and S. R. Charter. 1996. Bothidae: Lefteye flounders. Pp. 1357–1367 *in* The early stages of fishes in the California Current Region. (H. G. Moser, ed.), Coop. Fish. Invest. Atlas No. 33. Allen Press Inc., xii + 1505 pp.

Moser, H. G., and S. R. Sumida. 1996. Paralichthyidae: Lefteye flounders and sanddabs. Pp. 1325–1355 *in* The early stages of fishes in the California Current Region. (H. G. Moser, ed.), Coop. Fish. Invest. Atlas No. 33. Allen Press Inc., xii + 1505 pp.

Nelson, J. S. 1994. Fishes of the world. Third edition. John Wiley & Sons, Inc., xvii + 600 pp.

Norman, J. R. 1934. A systematic monograph of the flatfishes (Heterostomata), Vol. I. Psettodidae, Bothidae, Pleuronectidae. Brit. Museum (Natural History), 459 pp.

Richardson, S. L., and W. G. Pearcy. 1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fishery Bull. (U.S.) 75:125–145.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1991. Common and scientific names of fishes from the United States and Canada. 5th edition. American Fisheries Society Spec. Publ. 20. 183 pp.

Smith, P. E. 1995. A warm decade in the Southern California Bight. California Cooperative Oceanic Fisheries Investigations Reports 36:120–126.

Sommer, C. 1995. Pleuronectidae. Pp. 1381–1385 *in* Guía FAO para la identificacíon de especies para los fines de la pesca. Pacífico centro-oriental. Vol. III. Vertebrados – Parte 2, (W. Fischer, W. Schneider, C. Sommer, K. E. Carpenter, and V. H. Niem, eds.), United Nations, Food and Agriculture Administration, xiii + 1,813.

Accepted for publication 21 December 2000.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 144–148

First record of the sabertooth blenny, *Plagiotremus azaleus,* in California with notes on its distribution along the Pacific coast of Baja California

Daniel J. Pondella, II and Matthew T. Craig

Vantuna Research Group, Department of Biology,
Occidental College Los Angeles, California 90041

On 8 January 1998, while performing monthly ichthyological transects in King Harbor, Redondo Beach, California (latitude 33°50.5′ N, Longitude 118°24.0′ W), the senior author observed two individual sabertooth blennies, *Plagiotremus azaleus,* along the inside of the outer breakwater and along the Portofino reef at a depth of 1.5 m (Pondella and Stephens 1994). The water temperatures were 19.8° and 18.8° C, respectively. Since the initial sighting, sabertooth blennies were not observed again for another eight months in spite of continual monitoring. After 17 August 1998 they were observed while performing routine transects until 3 February 1999 along the Portofino reef in variable numbers ranging from one to six (Table 1). These fishes were observed in a temperature range from 13° to 24.5° C (Table 1). On 18 August 1998, we observed three sabertooth blennies along the Portofino reef and one was captured using a hand net and deposited at the Scripps Institute of Oceanography fish collection (SIO98-263) (Fig. 1). The specimen measured 59.8 mm SL and 68.3 mm TL (Table 2).

The previously reported range of the sabertooth blenny was the lower Gulf of California to Peru and did not include the Pacific coast of Baja California (Thomson, et al. 1979; Allen and Robertson 1994; Grove and Lavenberg 1997). The occurrence of the sabertooth blenny in Santa Monica Bay, represents a substantial range extension of approximately 1450 km. It is not, however, the only siting of this blenny outside of its historic range. It was also reported in a serpulid tube at the center island of Islas Benitos, Baja California, Sur on 5 August 1998 (R. N. Lea pers. comm.). On 4 November 1998 while diving on a cooperative (between CICESE, University of Baja California and University of California, Santa Barbara) research trip, Jennifer Casselle observed and subsequently captured a sabertooth blenny at Chester Rock, Punta Eugenia, Baja California, Sur, (Latitude: 27° 52.19″ N, Longitude: 115° 2.72″ W). On the same expedition another was observed at Point Augustine, Cedros Island (latitude 28° 4.46″ N, longitude 115° 20.50 W) (D. Schroeder pers. comm.). The specimen at Punta Eugenia measured 59.3 mm SL and 70.6 mm TL (SIO00-4) (Table 2). All characters, counts and measures for these two fishes are consistent with those values reported for the sabertooth blenny, considering that this is the only eastern Pacific representative of this group (Smith-Vaniz 1976), identification was straightforward.

The sabertooth blennies of the tribe Nemophini (Perciformes: Blenniidae) represent the most specialized group of the combtooth blennies. The tribe is an intriguing group of marine reef fishes found almost exclusively at tropical and subtropical latitudes to a depth of 25 m. Unlike most blenniids, the sabertooth blennies devote much time to hovering above the substrate or actively swimming

Table 1. Characters, counts and measurements for two specimens of sabertooth blenny, *Plagiotremus azaleus,* from southern and Baja California. Lengths are given in millimeters.

Characters, counts and measurements	Specimens SIO98-263	Specimens SIO00-4
Dorsal Fin	VIII, 32	VIII, 33
Anal fin	II, 27	II, 26
Pectoral fin	12	12
Procurrent caudal fin rays	6–8 + 6–8	5–6 + 5–7
Pelvic fins	present	present
Incisors on upper jaw	30	32
Incisors on lower jaw	54	55
Incisor ratio	1.8	1.7
Shape of dentary incisors	blunt	blunt
Shape of snout	conical	conical
Snout pigmentation	uniform	uniform
Interorbital pores	2	2
Supraorbital pores	2	2
Mandibular pores	2	2
Bony spur on innermost anal fin rays	absent	absent
Length of outer lobes of caudal fin	elongate	elongate
Dorsal fin stripe	present	present
Standard length	59.8	60.6
Total length	68.3	71.6
Preanal length	25.0	23.7
Caudal fin length	12.7	13.3

in the water column, they have a well-developed swim bladder, which aids in their semipelagic behavior (Smith-Vaniz 1976). Uncommonly large dentary canines used primarily in defense and intraspecific competition characterize *Plagiotremus,* one of five Nemophini genera. These thin and wedge shaped canines are capable of some movement and are apomorphic along with the lack of both premaxillary canine teeth and a lateral line. With the exception of a single eastern Pacific species, the sabertooth blenny, the tribe is restricted to the Indo-Pacific region.

Originally placed in the genus *Runula* by Jordan and Bollman (1889), the

Table 2. Date, number of individuals, temperature, and location of observation for the sabertooth blenny, *Plagiotremus azaleus,* outside of the Gulf of California. OB = outer breakwater, PR = Portofino reefs in King Harbor, Redondo Beach, CA, as described by Pondella and Stephens (1994).

Date	No. individuals	Location	Temperature (°C)
January 8, 1998	2	(1) OB, (1) PR	19.8, 18.8
August 5, 1998	1	Islas Benitos, Baja Cal.	20.9
August 17, 1998	2	PR	24.5
October 29, 1998	3	PR	16.8
November 4, 1998	3	Punta Eugenia, Baja Cal.	20.0
November, 1998	1	Cedros Island, Baja Cal.	19.0
November 19, 1998	3	PR	16.2
December 15, 1998	3	PR	13.8
January 7, 1999	6	PR	14.0
February 3, 1999	3	PR	13.0

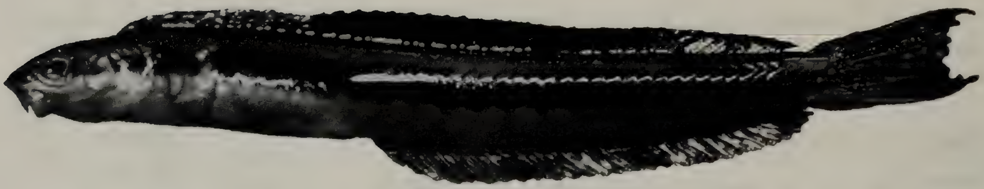


Fig. 1. Left lateral view of the sabertooth blenny, *Plagiotremus azaleus,* (59.8 mm SL, SIO98-263) captured in King Harbor, Redondo Beach, California on 18 August 1998. Photograph by Daniel J. Pondella, II.

holotype (USNM 44299) was collected at Indefatigable Island, Galápagos. Much confusion has been noted in the nomenclature of this species, primarily due to the conspicuous color phase shift from a banded juvenile phase to a striped adult phase. *Runula azaleus* was placed in *Plagiotremus* by Smith-Vaniz (1976) based upon a single apomorphic character described as "snout of adults fleshy, conical." Smith-Vaniz (1976) included a key to the genera and species of Nemophini and he did recognize *Runula* as a subgenus of *Plagiotremus* as five of the 11 species of *Plagiotremus,* including the sabertooth blenny, share the derived snout shape described above.

SCUBA divers can easily identify the sabertooth blenny and it is especially striking within the temperate reef community. Distinguished by its elongate body, cone-shaped snout, and bright yellow and blue stripes, the sabertooth blenny is easily differentiated from other members of eastern Pacific reef fish communities with the exception of the initial phase of the Cortez rainbow wrasse, *Thallasoma lucasanum* (Perciformes: Labridae). The sabertooth blenny only superficially resembles the Cortez rainbow wrasse, but differs in lacking the characteristic red underside of the wrasse, being clearly less deep bodied, and having an inferior mouth (rather than terminal).

While sabertooth blennies are known to aggregate with adult Cortez rainbow wrasses, they are not an aggressive mimic of the parasite-cleaning behavior of the juveniles (Hobson 1969). The three types of classical mimicry (Batesian, Müllerian and aggressive), may be found in *Plagiotremus* as well as in the allied blenniid genera *Aspidontus, Ecsenius,* and *Petroscirtes.* The classical example of aggressive mimicry comes from *Aspidontus taeniatus,* which has both juvenile and adult color phases similar to the labrid *Labroides dimidiatus* that establishes parasite cleaning stations for larger fishes. This allows *A. taeniatus* protection so it can approach larger fishes and bite the fins (Randall and Randall 1960). *Plagiotremus rhynorhynchos* also aggressively mimics this symbiotic cleaner wrasse and will ambush larger fishes on its own biting off pieces of fins, scales and mucous while they are feeding (Randall et al. 1996). This aggressive behavior is what has been observed for *P. azaleus* which is known to strike larger fishes from below and behind removing dermal material from the startled animal (Hobson 1969). Batesian mimicry may be due to a noxious taste, which has partially been demonstrated for *P. townsendi,* making them unpalatable to predators (Springer and Smith-Vaniz 1972). There is strong resemblance between the *P. laudandus* species group and the sympatric species of *Meiacanthus,* the fangblennies, and this may be an example of Müllerian mimicry (Smith-Vaniz 1976). Thus, this genus is of considerable intrigue in the study of the behavioral evolution of mimicry.

These fishes are diurnal reef species, which shelter within burrows of worm or mollusk tubes on the reef (Hobson 1965). The individuals captured and observed at all locations were adults, as the maximum reported length is 102 mm TL (Hobson 1969; Thomson et al. 1979). Similar to most blennies, the sabertooth blenny is oviparous and deposits its eggs in a parental guarded nest followed by a pelagic larval stage (Watson 1996). There is limited larval data available from the CalCOFI ichthyoplankton surveys, which describe sabertooth blenny larvae only from the Gulf of California and to the south (Watson 1996; H. Geoffrey Moser, pers. comm.). The larvae do have similar preflexion (2.1–5.6 mm), postflexion (7.2–13.6 mm) and juvenile (26.8–33.0 mm) lengths with respect to the other California blennies and may have a fairly extended larval period. For the southern California blennies the larval period for the mussel blenny, *Hypsoblennius jenkinsi,* was 34–56 days (mean = 44) and 46–79 days (mean = 66) for the rockpool blenny, *H. gilberti* (Stephens et al. 1970; Ninos 1984). The mussel blenny matures in the laboratory in 141 days after hatching (Stevens and Moser 1982). Considering the life history characters of this and confamilial species (an extended larval period, small size, habitat specificity and early maturity), the northern movement of this species was undoubtedly facilitated by larval drift during the very large 1997–98 El Niño Southern Oscillation event (Chavez et al. 1999). The observance of these fishes over such a wide geographic area and relatively long temporal period suggests that their presence in the warm temperate fauna of the San Diegan Province is not anomalous. However the continued success of the sabertooth blenny in Southern California is unknown.

Acknowledgements

The following research would not have been possible without the assistance of the following persons: John S. Stephens, Jr. of the Vantuna Research Group; Robert N. Lea of the Department of Fish and Game; Donna Schroeder, Jennifer Casselle and Milton Love of the Marine Science Institute, University of California, Santa Barbara; Jorge A. Rosales Casian and Oscar Sosa Nishizaki of CICESE; H. Geoffrey Moser of the National Marine Fisheries Service; the support of Wayne Ishimoto and Chevron Products Company; and the curatorial assistance of Richard H. Rosenblatt, H. J. Walker, and Cindy Klepadlo at the Scripps Institute of Oceanography.

Literature Cited

Allen, G. R. and D. R. Robertson. 1994. Fishes of the tropical eastern Pacific. University of Hawaii Press, Honolulu. xix + 332 p.

Chavez, F. P., P. G. Strutton, G. E. Friederich, R. A. Feely, G. C. Feldman, D. G. Foley, and M. J. McPhaden. 1999. Biological and chemical response of the equatiorial Pacific ocean to the 1997–98 El Niño. Science. 286:2126–2131.

Grove, J. S. and R. J. Lavenberg. 1997. The fishes of the Galápagos Islands. Stanford University Press, Stanford, California. xliv + 863 p.

Hobson, E. S. 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965(3):291–302.

———. 1969. Possible advantages to the blenny *Runula azalea* aggregating with the wrasse *Thalassoma lucasanum* in the tropical eastern Pacific. Copeia 1969(1):191–93.

Jordan, D. S. and C. H. Bollman. 1890. Scientific results of explorations by the U. S. Fish Commission steamer Albatross. No. IV. Descriptions of new species of fishes collected at the Galápagos Islands and along the coast of the United States of Colombia, 1887–88. Proc. U. S. Natl. Mus. 12(770):149–83.

Ninos, M. 1984. Settlement and metamorphosis in *Hypsoblennius* (Pisces, Blenniidae). Ph.D. dissertation, University of Southern California, Los Angeles, 181 p.

Pondella, D. J., II, and J. S. Stephens, Jr. 1994. Factors affecting the abundance of juvenile fish species on a temperate artificial reef. Bull. Mar. Sci. 55(2–3):1216–1223.

Randall, J. E., G. R. Allen, and R. C. Steene. 1996. Fishes of the Great Barrier Reef and Coral Sea. University of Hawaii Press, Honolulu, HI. xx + 557 p.

Randall, J. D. and H. A. Randall. 1960. Examples of mimicry and protective resemblance in tropical marine fishes. Bull. Mar. Sci. Gulf and Carib. 10(4):444–480.

Smith-Vaniz, W. F. 1976. The saber-toothed blennies, tribe Nemophini (Pisces: Blenniidae). Acad. Nat. Sci. Phila. Monog. 19. 196 p.

Springer, V. G. and W. F. Smith-Vaniz. 1972. Mimetic relationships involving fishes of the family Blenniidae. Smithsonian Contributions to Zoology 112. 36 p., 4 figs., 7 pls.

Stephens, Jr., J. S., R. K. Johnson, G. S. Key, and J. E. McCosker. 1970. The comparative ecology of three sympatric species of California blennies of the genus *Hypsoblennius* Gill (Teleostomi, Blenniidae). Ecological Monographs 40(2):213–233.

Stevens, E. G. and H. G. Moser. 1982. Observations on the early life history of the mussel blenny, *Hypsoblennius jenkensi,* and the bay blenny, *Hypsoblennius gentilis,* from specimens reared in the laboratory. Calif. Coop. Ocean. Fish. Inv. Rep. 23:269–275.

Thomson, D. A., L. T. Findley, and A. N. Kerstitch. 1979. Reef fishes of the Sea of Cortez. John Wiley and Sons, New York, New York. xvii + 302 p. + 32 pls.

Watson, W. 1996. Blenniidae: combtooth blennies. Pp. 1182–1199 *in* H. Geoffrey Moser ed., The Early Stages of Fishes in the California Current Region. California Cooperative Oceanic Fisheries Investigations Atlas No. 33., Allen Press, Inc., Lawrence, Kansas. xii + 1505 p.

Accepted for publication 19 June 2000.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 149–152

Addition of Blacklip Dragonet, *Synchiropus atrilabiatus* (Garman, 1899) (Pisces: Callionymidae) to the California Ichthyofauna

Ami K. Groce,[1] Richard H. Rosenblatt,[2] and M. James Allen[3]

[1]*City of San Diego, Metropolitan Wastewater Department, Environmental Monitoring and Technical Services Division, San Diego, California 92106*
[2]*Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California, 92093-0208*
[3]*Southern California Coastal Water Research Project, Westminster, California, 92683*

Dragonets (family Callionymidae) are small, often colorful, benthic fishes found in coastal tropical waters of the Atlantic, Indian, and Pacific Oceans, but primarily in the Indo-West Pacific (Nelson 1994). The systematics of this family are not well known, with numbers of taxa ranging from 8 genera and 40 species to 19 genera and 139 species (Grove and Lavenberg 1997). The only dragonet known from the Eastern Pacific is *Synchiropus atrilabiatus* (Garman 1899), which is found primarily off Mexico and Central America (Grove and Lavenberg 1997).

Following the 1997–1998 El Niño, two specimens of the blacklip dragonet were collected in the Southern California Bight (SCB) by semiballoon (7.6-m wide headrope) otter trawls with 1.2-cm cod-end mesh. The first specimen (56 mm SL) was collected on 23 July 1998 off Santa Catalina Island (latitude 33°17.68′N, longitude 118°17.00′W) at a depth of 97 m, during the Southern California Bight 1998 Regional Survey (Bight'98), a bight-wide survey of the mainland and island shelves of southern California. The second specimen (90 mm SL) was collected on January 19, 1999 off Point Loma, California (latitude 32°37.54′N, longitude 117°19.37′W) at a depth of 100 m. It was captured at one of the City of San Diego, Metropolitan Wastewater Department, Environmental Monitoring and Technical Services' long-term, fixed-location trawl monitoring stations, which has been sampled quarterly since July 1991. City of San Diego marine biologists brought this specimen to the attention of the second author (RHR), who identified it as *Synchiropus atrilabiatus.* This was the first specimen identified from California waters although it was the second specimen collected. The third author (MJA) identified the first-caught specimen later when voucher specimens collected during the Bight'98 survey were sent to SCCWRP for taxonomic confirmation. Both specimens had similar meristics (Table 1) and have been catalogued in the SIO Marine Vertebrates Collection: SIO 99-1 (Point Loma) and SIO 00-79 (Santa Catalina Island).

The previous published geographic range of this species was from Bahiá Magdalena, Baja California Sur, Mexico and the Gulf of California to Talara, Peru, including Gorda Banks (off Cabo San Lucas, Baja California Sur, Mexico), Cocos Island, and the Galápagos Islands (Fricke 1981; Cruz-Aguero et al. 1994). The capture of *Synchiropus atrilabiatus* at Santa Catalina Island represents a range extension of 1,250 km north of its northernmost published record at Bahiá Mag-

Table 1. Location and meristic data for *Synchiropus atrilabiatus* specimens collected in southern California in 1998 and 1999.

	Specimens	
Category	SIO 00–79	SIO 99–1
Collection Information		
Date	23 July 98	19 January 99
Location	Santa Catalina Island, CA	off Point Loma, CA
Latitude, Longitude	33°17.68′ N, 118°17.00′ W	32°37.54′ N, 117°19.37′ W
Depth (m)	97	100
Standard Length (mm)	56	90
Merisitic Counts		
Dorsal Fin Elements	IV, 9	IV, 9
Anal Fin Rays	8	8
Pectoral Fin Rays	20	22
Pelvic Fin Elements	I, 5	I, 5
Principal Caudal Fin Rays	10	10

dalena, Mexico (latitude 24°35.0′N) (Cruz-Aguero et al. 1994; Love et al. 1996[1]) and about 650 km from its previous northernmost unpublished occurrence (i.e., Bahiá Playa Maria, Baja California, Mex.; latitude 28°52.0′N, longitude 114°30.0′W; 1 September 1952; SIO 52-60).

Synchiropus atrilabiatus occurs on soft bottoms on the mainland and island shelf. Benthic individuals range in depth from 12 to 150 m in sand and mud habitats, and to a lesser degree in coral rubble (Grove and Lavenberg 1997). Maximum known size of adults is 121 mm (SIO 84-80). This species is oviparous with planktonic eggs and larvae (Watson 1996). Larvae are taken throughout the year, with young larvae collected primarily during summer (Watson 1996). Although the species transforms from larva to juvenile at 8.3–12.5 mm (Watson 1996), pelagic juveniles up to 39 mm SL have been taken in midwater (SIO 72-342), and both larvae and pelagic juveniles have been taken near the surface offshore to 300 km over water depths of 4,000 m or more (Grove and Lavenberg 1997).

Synchiropus atrilabiatus has a cottiform body with a small mouth (Figure 1) and superficially resembles a sculpin (family Cottidae). It differs from all sculpins in having the gill opening reduced to a pore on the dorsal surface behind the head (Figure 1); sculpins have relatively large lateral gill openings. It is scaleless with a pointed snout and highly protrusible upper jaws. Characteristics of *S. atrilabiatus* that distinguish it from other callionymids include numerous small dark blotches on body, a dorsal fin with dark oval blotches between the third and forth spines, black coloration on the lower half of the anal fin, and a black margin on the upper jaw (Fricke 1981). Fin element ranges are the following: dorsal fin (IV,8–9), anal fin (7–8), pectoral fins (18–23), pelvic fins (I,5), principal caudal rays (5+5), and procurrent caudal rays (2–3 upper, 2 lower). There are 6 branchiostegal rays.

---

[1] Love, M. S., L. Thorsteinson, C. W. Mecklenburg, and T. A. Mecklenburg. 1996. A checklist of marine and estuarine fishes of the North East Pacific, from Alaska to Baja California. National Biological Service. Located at website http://id-www.ucsd.edu/ lovelab/home.html

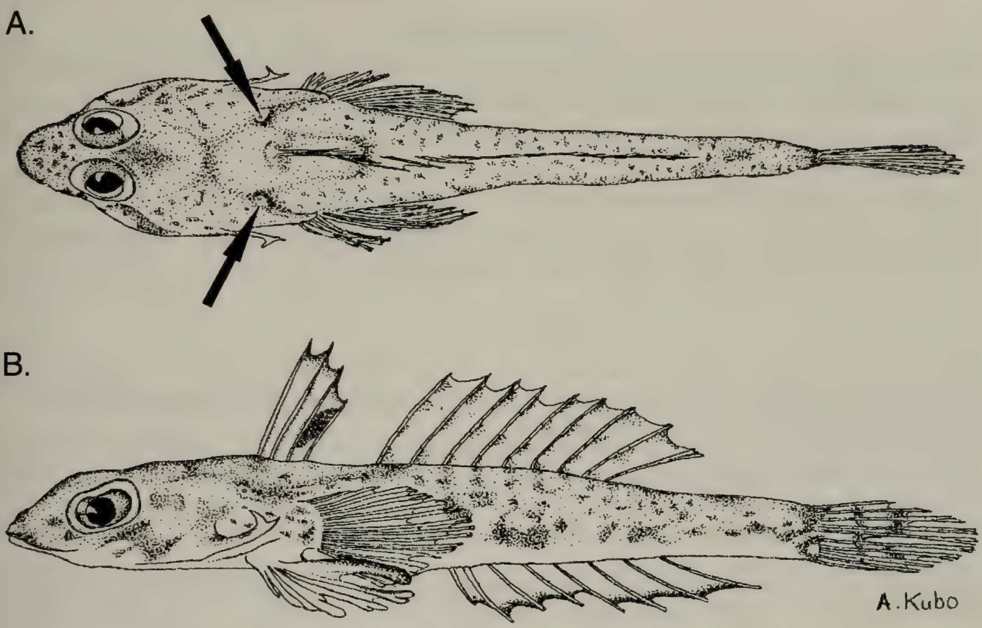


Fig. 1a and b. Blacklip dragonet (*Synchiropus atrilabiatus*). Top (a) and side view (b) of specimen from Santa Catalina Island, 56 mm SL; SIO 00-79 (drawing by Atsuhiro Kubo). Arrows indicate diagnostic gill pore on dorsal surface behind the head.

The appearance of *Synchiropus atrilabiatus* in the waters of the Southern California Bight at the time of collection may be related to the physical oceanographic conditions associated with the 1997–1998 El Niño. This was just one of many tropical species collected for the first time in California after the warm water intrusion that was first detected in Southern California during July and August 1997 (Lea and Rosenblatt 2000). These fishes may have come into the area as larvae or juveniles with the warm water mass that moved up from the south. While no ages were determined for the two specimens discussed here, they were collected at relatively small sizes (56 mm in July 1998 and 90 mm in January 1999) compared to the maximum size of the largest known *S. atrilabiatus* (121 mm; SIO), as well as the maximum family size (25 to 30 cm; Bussing and Lopez 1994; Grove and Lavenberg 1997). If juveniles are pelagic to about 39 mm (as indicated by SIO collection data), the first specimen may have settled to the bottom in spring of 1998. The second specimen may have settled at this time also and grown to its length at capture in nearly a year's time; however, the growth rate of this species is not known.

The common name 'blacklip dragonet' was suggested by the second author (RHR) in reference to its black upper lip and its scientific name *atrilabiatus* (black lip). Other English common names for this species include 'sleepy dragonet' (Bussing and Lopez 1994) and 'antler dragonet' (Grove and Lavenberg 1997); in Spanish, it is known as 'gobio vistoso' (Bussing and Lopez 1994) and 'dragonito de asta' (Grove and Lavenberg 1997). We recommend 'blacklip dragonet' as an English common name for this species as this name has more diagnostic value than the other common names.

Acknowledgments

The authors thank Dr. Michael Franklin (Southern California Marine Institute) and Steven Lagos and Eric Nestler (both of the City of San Diego, Metropolitan Wastewater Department, Ocean Monitoring Program) for recognizing the first and second specimens, respectively, as unusual. We thank Atsuhiro Kubo for contributing the drawings of the Santa Catalina Island specimen. We also thank Richard Feeney and Jeffery Siegel of the Natural History Museum of Los Angeles for collection information on *Synchiropus atrilabiatus.*

Literature Cited

Cruz-Aguero, J. del la, F. Galvan-Magana, L. A. Abitia-Cardenas, J. Rodriquez-Romero, and F. J. Gutiemez-Sanchez. 1994. Systematic list of marine fishes from Bahiá Magdalena, Baja California Sur (Mexico). Cienc. Mar. 20:17–31.

Bussing, W. A., and M. I. Lopez S. 1994. Demersal and pelagic inshore fishes of the Pacific Coast of lower Central America. Special Publication of the Revista de Biologia Tropical, San Jose, Costa Rica. 164 pp.

Fricke, R. 1981. Revision of the genus *Synchiropus:* Theses Zoologicae Vol. I. J. Cramer, Braunschweig. 194 pp.

Garman, S. 1899. The fishes *in* Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galápagos Islands by the U. S. Fish Commission steamer "Albatross" during 1891. No. XXVI. Mem. Mus. Comp. Zool. v. 24. 431 pp. + 85 pl.

Grove, J. S. and R. J. Lavenberg. 1997. The Fishes of the Galápagos Islands. Stanford University Press. 936 pp.

Lea, R. N. and R. H. Rosenblatt. 2000. Observations on fishes associated with the 1997–1998 El Niño off California. CalCOFI Reports Vol 41:117–129.

Nelson, J. S. 1984. Fishes of the World, Third Edition. John Wiley and Sons, Inc. xvii + 600 pp.

Watson, W. 1996. Callionymidae: Dragonets. Pages 1205–1207 *in* The Early Stages of Fishes in the California Current Region. Coop. Fish. Invest. Atlas. No. 33 (H. G. Moser, ed.), Allen Press Inc. 1,505 pp.

Accepted for publication 21 December 2000.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 153–155

Addition of the Calico Lizardfish, *Synodus lacertinus* Gilbert, 1890 (Pisces: Synodontidae) to the Ichthyofauna of the Southern California Bight

Ami K. Groce, Steven L. Lagos, and Eric C. Nestler

City of San Diego, Metropolitan Wastewater Department, Environmental Monitoring and Technical Services Division, Point Loma, California 92106

Lizardfishes (Synodontidae) are small to moderate-sized fishes with elongate, cylindrical bodies and large, spiny toothed, lizard-like mouths. They are common benthic fishes found in the Atlantic, Indian and Pacific Oceans (Nelson 1994). *Synodus* is the only genus known from the Eastern Pacific, and is represented by five species (*S. evermanni, S. lacertinus, S. lucioceps, S. sechurae,* and *S. scituliceps;* Allen and Robertson 1994; Grove and Lavenberg 1997). Only one of the five species, the California lizardfish, *S. lucioceps,* has previously been reported from the Southern California Bight (SCB).

On October 9, 1998, a single specimen of the calico lizardfish, *Synodus lacertinus,* was collected by small (7.6 m wide headrope) semiballoon otter trawl during a routine survey performed by the City of San Diego's Marine Biology Laboratory (Metropolitan Wastewater Department, Environmental Monitoring and Technical Services Division). The specimen was captured off Playas de Tijuana (approx. 6 km south of the United States-Mexico boundary) (latitude 32°28.35′ N and longitude 117°10.50′ W) at a depth of 27 m over sandy substrate. The fish was measured and photographed, then deposited in the Marine Vertebrates Collection, Scripps Institution of Oceanography (SIO 99-28). It measured 129 mm standard length (SL) and 145 mm total length (TL) and had the following counts: dorsal fin elements (11), anal fin rays (8), pectoral fin rays (11), pelvic fin elements (8) and lateral line scales (61). The specimen was identified by R. H. Rosenblatt as *Synodus lacertinus* Gilbert, 1890 (Figure 1). The calico lizardfish has also been referred to as the sauro lizardfish (Cruz-Aguero et al. 1994, Bussing and Lavenberg 1995), the banded lizardfish (Grove and Lavenberg 1997), and the reef lizardfish (Allen and Robertson 1994).

The previous published geographic range of this species was from Bahia Magdalena, Baja California Sur, Mexico (Cruz-Aguero et al. 1994; Love et al. 1996[1]) and the Gulf of California to Peru, including the Cocos and the Galapagos Islands (Bussing and Lavenberg 1995; Grove and Lavenberg 1997). Unpublished occurrences of this species farther north than Bahía Magdalena include a specimen collected in February 1964 at San Pablo Point (latitude 27°13.0′ N; SIO 64-68) and a photo of *S. lacertinus* from Islas San Benito (approx latitude 28° N; R. N. Lea, pers comm.). The capture of *S. lacertinus* near the United States-Mexico

---

[1] Love, M. S., L. Thorsteinson, C. W. Mecklenburg, and T. A. Mecklenburg. 1996. A checklist of marine and estuarine fishes of the North East Pacific, from Alaska to Baja California. National Biological Service. Located at website http://id-www.ucsd.edu/lovelab/home.html

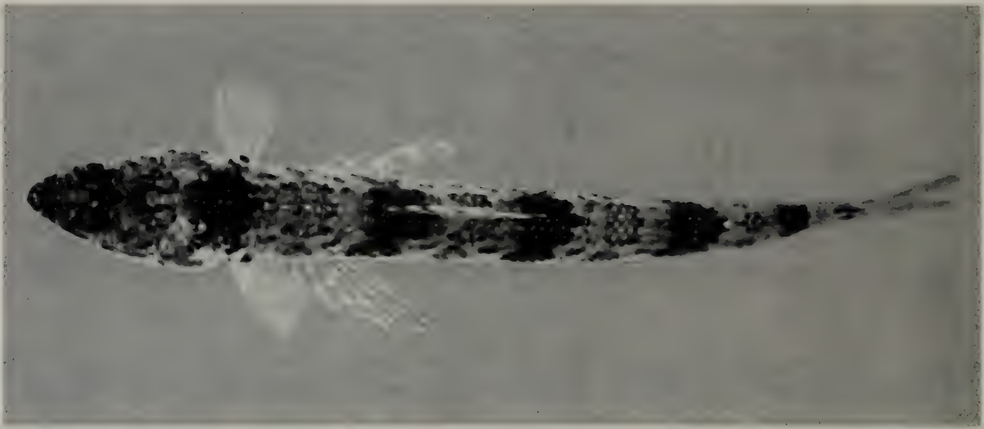


Fig. 1. Calico lizardfish (*Synodus lacertinus*), dorsal aspect. Specimen from off Playas de Tijuana, 129 mm SL; SIO 99-28. Photo taken by Ron Velarde.

boundary represents a range extension of greater than 500 km from these locations off central Baja California, Mexico.

Characteristics of *Synodus lacertinus* that distinguish it from other eastern Pacific synodontids include most notably five broad dark bars across the dorsum (Grove and Lavenberg 1997). These dark bars make *S. lacertinus* quite distinct from *S. luciosceps,* which is the only lizardfish commonly found in the SCB. Other diagnostic characters include an upper jaw larger than lower jaw, short snout (especially compared to *S. lucioceps*), dorsal and caudal fins with a series of oblique stripes, and a wide head (as broad as long) (Allen and Robertson 1994; Bussing and Lavenberg 1995; Grove and Lavenberg 1997). *Synodus lucioceps* is also quite distinct from *S. lacertinus* in that it has a diagnostic yellow coloration on its gill membranes and pelvic fins. The other Eastern Pacific *Synodus, S. evermanni, S. scituliceps,* and *S. sechurae* (as well as *S. lucioceps*) all have fairly dull coloration in comparison to *S. lacertinus.* In addition to differences in coloration, these species have different meristics (see Allen and Robertson 1994, Bussing and Lavenberg 1995, Grove and Lavenberg 1997).

The appearance of *Synodus lacertinus* in the Southern California Bight may be related to the physical oceanographic conditions associated with the 1997–1998 El Niño. This was just one of many tropical species collected for the first time in the Bight after the warm water intrusion that was first detected in July and August 1997 (Lea and Rosenblatt 2000). Our fish may have come into the area with the warm water mass that moved up from the south. Although the size of this specimen, at 145 mm TL, was very close to its known maximum length of 160 mm TL (Allen and Robertson 1994), it is possible that the fish either moved into the area with this El Niño event as an adult, or with a previous event as a larvae or juvenile.

Acknowledgments

The authors are indebted to R.H. Rosenblatt for identifying this specimen, and to the curatorial assistance of H.J. Walker, C. Klepadio and P. Hastings at the Scripps Institution of Oceanography. We would also like to thank R. Feeney and

J. Siegel of the Natural History Museum of Los Angeles for collection information on *Synodus lacertinus.* We would like to acknowledge the critical review and assistance of M.J. Allen (Southern California Coastal Water Research Project), and information provided by R.N. Lea (California Department of Fish and Game).

Literature Cited

Allen, G. R. and D. R. Robertson. 1994. Fishes of the Tropical Eastern Pacific. University of Hawaii Press. 332 pp.

Bussing, W.A., and R.L. Lavenberg. 1995. Synodontidae. Pages 1625–1628 *in* Guia FAO para la identificacion de especies para los fines de la pesca Pacifico Centro-Oriental: Volume III, Vertebrados Parte 2. W. Fisher, W., F. Krupp, W. Schneider, C. Sommer, K. E. Carpenter, and V. H. Niem (eds), United Nations Food and Agriculture Organization, Roma, It.

Cruz-Aguero, J. del la, F. Galvan-Magana, L. A. Abitia-Cardenas, J. Rodriquez-Romero, and F. J. Gutiemez-Sanchez. 1994. Systematic list of marine fishes from Bahiá Magdalena, Baja California Sur (Mexico). Cienc. Mar. 20:17–31.

Gilbert, C. H. 1890. A preliminary report on the fishes collected by the steamer Albatross on the Pacific Coast of North America during the year 1889, with descriptions of twelve new genera and ninety-two new species. Proc. U.S. Natl. Mus. V.13 (797):49–126.

Grove, J. S. and R. J. Lavenberg. 1997. The Fishes of the Galápagos Islands. Stanford University Press, 936 pp.

Lea, R. N. and R. H. Rosenblatt. 2000. Observations on fishes associated with the 1997–1998 El Niño off California. CalCOFI Reports Vol 41:117–129.

Nelson, J. S. 1994. Fishes of the World, Third Edition. John Wiley and Sons, Inc. xvii + 600 pp.

Accepted for publication 25 January 2001.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 156–159

First Record of the Pacific Cornetfish, *Fistularia corneta* Gilbert and Starks 1904, a New Species to the Southern California Fauna During the 1997–1998 El Niño

Michael D. Curtis[1] and Kevin T. Herbinson[2]

[1]*MBC Applied Environmental Sciences, Costa Mesa, California 92626*
[2]*Southern California Edison Company, Rosemead, California 91770*

On 7 May 1998, two small cornetfish (319 and 345 mm total length) were taken from the cooling water screenwell in front of the circulating water gates at the former Southern California Edison's Huntington Beach Generating Station (now AES Huntington Beach) during a routine fouling control operation. They were initially thought to be the reef cornetfish, *Fistularia commersonii;* however, critical examination indicated that these two specimens are the Pacific cornetfish, *Fistularia corneta* Gilbert and Starks 1904, a new addition to the California fauna.

The occurrence of *F. corneta* at the Huntington Beach Generating Station intake in Huntington Beach, Orange County, California (33°38.37′ N and 117°58.98′ W) represents a range extension of approximately 836 km from its previously listed northern most record at San Hipolito, Baja California, Mexico (26°58.0′ N and 113°58.2′ W). On 27 August 1956, 11 specimens of *F. corneta,* ranging from 111 to 190 mm, were collected from Bahia San Hipolito (from SIO Collection No. 64–750[1]). The Huntington Beach specimens, therefore, represent an extension of approximately 836 km from that location.

The sea floor directly offshore of the Huntington Beach Generating Station is relatively smooth and sediments are composed of mostly fine-to-medium grained sand, with isobaths parallel to the coastline. The intake is located about 500 m offshore on a smooth sandy bottom at a depth of approximately 8 m. Pacific cornetfish typically are taken over smooth bottoms (Fritzche 1976) and are referred to as the deepwater cornetfish in the Gulf of California, as they typically occur in water depths greater than 30 m (Thomson *et al.* 1979). Its previous published range is from the outer coast of Baja California near Bahia San Hipolito to Peru and the offshore islands (Hildebrand 1946, Thomson *et al.* 1979). They are frequently collected in otter trawls.

Cornetfishes (Fistulariidae) have an elongate, depressed body with long tubular snout, short oblique mouth, minute teeth, single dorsal fin located posterior on body above anal fin and a forked caudal fin with a long medial filament (Allen and Robertson 1994) (Figure 1). There are four species in the tropical and subtropical genus of *Fistularia.* Two of these, the reef cornetfish and the Pacific cornetfish, are found in the eastern Pacific (Fritzche 1976, Allen and Robertson 1994, Fritzche and Schneider 1995). The Pacific cornetfish differs from the reef cornetfish by having more dorsal, anal, and pectoral rays, usually 18 to 20, 17 to 18, and 16 to 18, respectively; reef cornetfish have dorsal rays of 15 to 17, anal

---

[1] Scripps Institution of Oceanography Marine Invertebrates Fish Collection. 2000. Website: www-sioadm.ucsd.edu/FM (*Fistularia corneta*) SIO number 64–750.

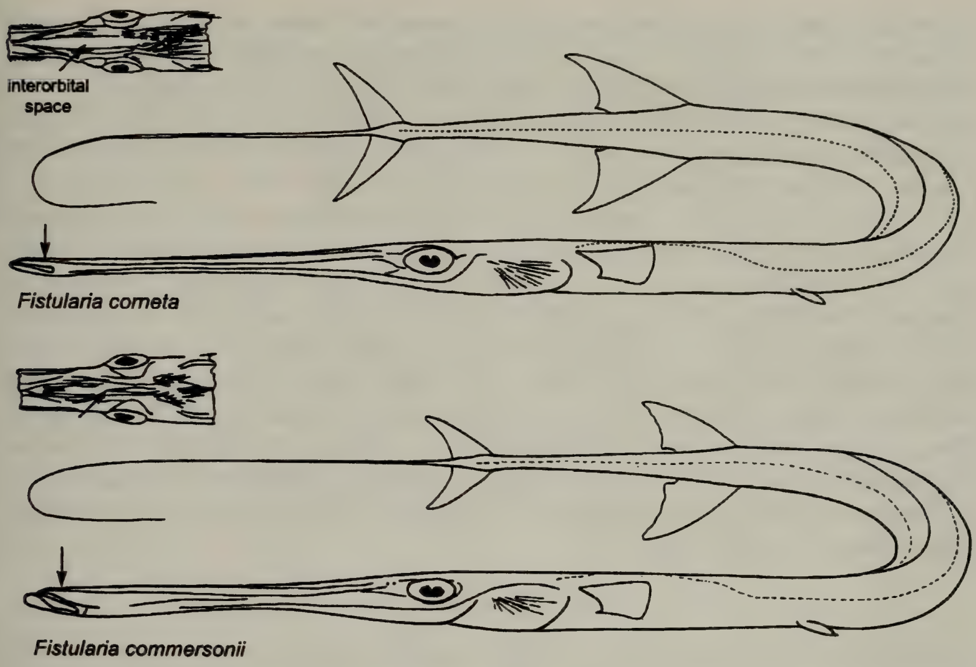


Fig. 1. Dorsal views of head and body of Pacific cornetfish (*Fistularia corneta*) and reef cornetfish (*Fistularia commersoni*) (Fig. from Bussing and Lopez 1994).

rays of 14 to 16, and pectoral rays of 13 to 15 (Thomson *et al.* 1979, Allen and Robertson 1994). Pacific cornetfish are reported to attain lengths of at least 700 mm, whereas reef cornetfish can grow to be at least 1500 mm in length (Allen and Robertson 1994, Fritzche and Schneider 1995). Specimens collected at Huntington Beach had meristics within the range of Pacific cornetfish (Table 1).

A definitive identification was made by looking at the interorbital area of the head. In Pacific cornetfish there is a wide smooth interorbital space, whereas longitudinal ridges are found in this same area in reef cornetfish. This is aptly illustrated in Bussing and Lopez (1994).

As has been documented with past El Niños, the advent of the El Niño of 1997–1998 brought new species of fish and invertebrates to the southern California waters (Wooster and Fluharty 1985, Lea and Rosenblatt 2000). Although it appears this cornetfish species may have a preference for slightly cooler waters

Table 1. Meristics of the two Huntington Beach specimens of Pacific cornetfish, *Fistularia corneta,* LACM 54542-1.

	Specimen	
	1	2
Total Length (mm) End of Filament	345	319
Biomass (g)	20	14
Dorsal, Fin Rays	18	18
Anal, Fin Rays	17	17
Pectoral, Fin Rays	17	18

found at depth, it is not unusual to find expatriate fishes from Baja California attracted to the vicinity of southern California power plant discharges. Ocean temperatures in the vicinity of the intake were 16.1° C on the day of capture, several degrees warmer than seasonally normal due to the effects of the El Niño. Typically, temperatures are also 4 to 5° C higher within 10 m of the power plant discharge plume, decreasing rapidly with distance (MBC1975). It is possible that the two specimens of *F. corneta* were attracted to the area due to the presence of warm water at the outfall. Alternatively, because it is known that the intake and discharge structures act as *de facto* artificial reefs attracting a variety of species of fish, the predatory cornetfish may have been present in the immediate area to forage on fishes associated with the high relief intake and discharge structures (Helvey and Dom 1981, Helvey and Smith 1985). Whatever their reason for being in the vicinity, they were inadvertently entrained by the strong inward flow of water at the intake tunnel and transported through the tunnel to the forebay of the power plant where they were subsequently impinged and collected.

The two specimens are deposited at the Natural History Museum of Los Angeles County, (LACM 54542-1).

Acknowledgments

We wish to thank M. J. Allen for his constant enthusiasm, identification of the two specimens, suggestions of literature, and critical review of the manuscript. We would also like to thank R.N. Lea and J. Siegel for their support and encouragement and critical reviews of the manuscript which have resulted in an improved paper. In addition, we would like to thank Southern California Edison, MBC *Applied Environmental Sciences,* and AES Huntington Beach Generating Station for supporting these studies.

Literature Cited

Allen, G.R., and D.R. Robertson. 1994. Fishes of the tropical eastern Pacific. University of Hawaii Press, xix + 332 pp.

Bussing, W.A., and M. I. Lopez S. 1994. Demersal and pelagic Inshore fishes of the Pacific coast of lower Central America: An illustrated guide. Rev. Biol. Trop; Spec. Publ., 164 pp.

Fritzsche, R. A. 1976. A review of the cornetfishes, genus *Fistularia* (Fistulariidae), with a discussion of intrageneric relationships and zoogeography. Bull. Mar. Sci., 26(2):196–204.

Fritzsche, R. A., and M. Schneider. 1995. Fistulariidae. Pp. 1104–1105 *in* Guia FAO para la identificacion de especies para los fines de la pesca. Pacifico centro-oriental. Vol. II. Vertebrados—Parte 1, (W. Fischer, W. Schneider, C. Sommer, K. E. Carpenter, and V. H. Niem, eds.), United Nations, Food and Agriculture Administration, xiii + 1,813 pp.

Gilbert, C.H., and E.C. Starks. 1904. The fishes of Panama Bay. Mem. Calif. Acad. Sci. v.4. 304 pp.

Helvey, M., and P. Dom. 1981. The fish population associated with an offshore water intake structure. Bull. So. Calif. Acad. Sci., 80(1):23–31.

Helvey, M., and R.W. Smith. 1985. Influence of habitat structure on the fish assemblage associated with two cooling-water intake structures in southern California. Bull. Mar. Sci., 37(1):189–199.

Hildebrand, S. F. 1946. A descriptive catalog of the shore fishes of Peru. Smithsonian Institution, U.S. Nat. Mus., Bulletin 189:150–152.

Lea, R. N., and R. H. Rosenblatt. 2000. Observation on fishes associated with the 1997–1998 El Niño off California. Calif. Coop. Ocean. Fish. Inves. Rep. 41:1178–129.

Marine Biological Consultants. 1975. The Marine Environment Offshore Huntington Beach Generating Station Orange County, California. First Quarterly Report, August 1975 Survey. Prepared for Southern California Edison Company. Mar. Bio. Consul., Costa Mesa, CA. 40 pp. + appendices.

Thomson, D. A., L.T. Findley, and A.N. Kerstitch. 1979. Reef fishes of the Sea of Cortez. John Whiley & Sons, Inc., NY., 302 pp.

Wooster, W.S., and D.L. Fluharty 1985. El Niño North: Niño Effects in the Eastern Subartic Pacific Ocean. Washington Sea Grant Prog., University of Washington, 312 pp.

Accepted for publication 21 December 2000.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 160–166

Records of Mexican Barracuda, *Sphyraena ensis,* and Scalloped Hammerhead, *Sphyrna lewini,* from Southern California Associated with Elevated Water Temperatures

Michael A. Shane

Hubbs-SeaWorld Research Institute, 2595 Ingraham Street, San Diego, California 92109

During the 1997–98 El Niño Southern Oscillation (ENSO), abnormally warm coastal waters occurred off southern California. Based on satellite imagery, the highest sea surface temperature anomalies recorded in southern California during this event were between 3 and 4°C. Monthly mean sea surface temperatures, recorded at the Scripps Institute of Oceanography (SIO) pier between 1916 and 1994, ranged from 14 to 21°C. Monthly mean sea bottom temperatures, also recorded at the SIO pier at a depth of 5 m between 1926 and 1994, ranged from 14 to 19°C. During previous warm water years, investigators documented changes in the ichthyofauna along the Pacific Coast (e.g., Hubbs and Schultz 1929; Walford 1931; Brooks 1987; Lea and Rosenblatt 1992; Lea and Walker 1995). I report here on two species of fish that were present off southern California correlated with elevated water temperatures generated by the 1997–1998 ENSO and by an anthropogenic source.

Sphyraena ensis

On 20 October 1997, multiple mesh gillnets were deployed on the bottom in a kelp forest north of Oceanside, California (latitude 33°17.65′N, longitude 117° 29.57′W), in an attempt to catch hatchery-reared white seabass, *Atractoscion nobilis,* released by the Ocean Resources Enhancement and Hatchery Program (OREHP). The following morning, an unfamiliar barracuda was retrieved from a net set at a depth of 14 m. Also on this morning, water samples were collected at depth at three sites in this area. The average bottom temperature of the water samples was 19.7°C. Furthermore, there were no other barracudas caught in this net or in two others set nearby. This fish was later identified by the author as a Mexican barracuda, *Sphyraena ensis* (Jordan and Gilbert 1882), and represents the first record from southern California. On 11 January 1998 another Mexican barracuda was taken by hook-and-line aboard the sportfishing vessel MV Dolphin II off La Jolla, California (latitude 32°51.0′N, longitude 117°16.0′W) in a water depth of 9 m. The sport fisherman also noted that the Mexican barracuda was schooling with the more common Pacific barracuda, *S. argentea.* This fish was turned over to the Marine Vertebrates Collection, Scripps Institution of Oceanography, and identified by R. H. Rosenblatt; it is catalogued as SIO 98-35. Subsequently, the identification of the specimen collected north of Oceanside was also verified by R. H. Rosenblatt and deposited in the Scripps collection as SIO 98-36. On 22 September 1998, three more Mexican barracuda were caught by the OREHP assessment program in a gillnet set on the bottom at a water depth of 4.5 m near La Jolla (latitude 32°48.28′N, longitude 117°16.08′W). These three

Table 1. Morphometric and meristic data for *Sphyraena ensis*[a]

	Specimen				
	SIO 98-35	SIO 98-36	HSWRI SE-1	HSWRI SE-2	HSWRI SE-3
Standard length (mm)	425.0	470.0	475.0	433.0	426.0
Head from tip of snout	32.9	30.2	29.3	30.0	30.0
Depth	14.3	14.8	15.2	12.7	13.2
Orbit	5.1	4.7	5.8	5.8	6.5
Insertion ventral spine from tip of snout	44.7	39.1	39.2	39.7	39.4
Spinous dorsal from snout	45.6	43.0	42.3	42.0	42.7
Soft dorsal from snout	76.5	72.1	71.4	71.8	72.1
Length of pectoral fin	13.0	10.6[b]	11.2	12.4	11.7
Longest dorsal ray	10.6	6.8[b]	9.7	11.3	10.5
Longest anal ray	10.0	7.3[b]	8.6	10.0	9.3
Number of dorsal rays and spines	V + I, 9	V + I, 9	V + I, 9	V + I, 9	V + I, 9
Number of anal rays and spines	II, 7	II, 7	II, 8	II, 8	II, 8
Number of scales	108	110	108	110	108

[a] Measurements follow those of Gilbert and Starks (1904). Morphometric characters, with the exclusion of standard length, are given in hundreds of standard length.

[b] Length of fin or ray on the left side of the body is incomplete.

specimens are presently being held at Hubbs-SeaWorld Research Institute. In addition, there were also several Pacific barracuda caught in the same net. The bottom water temperature, recorded from a water sample collected at depth on this morning, was 19.9°C. Counts and measurements for the five Mexican barracuda described above, following Gilbert and Starks (1904), are provided in Table 1.

During March or April 1998, Scott Aalbers photographed a school of seven barracuda in the shallow waters off La Jolla. These barracuda looked similar to the ones he had observed previously in Mexico. Due to the quality of the photograph, only two of the barracuda can be positively identified as Mexican barracuda. This identification is based on the observation that the pelvic fin, which is extended downward and away from the body in these two individuals, is attached directly below the posterior tip of the pectoral fin. Additionally, these two fish, as well as several others in the photograph, also have dark bars on their sides. Positive identification of the remaining fish in the photograph as Mexican barracuda could not be made due to the quality of the photograph and because this species has been previously observed schooling with the Pacific barracuda.

Four species of barracuda (family Sphyraenidae) occur in the eastern Pacific. Until now, only the Pacific barracuda had been reported to occur in the marine waters off California (Miller and Lea 1972; Robins et al. 1991a). The Mexican barracuda, normally found in the Panamic Zoogeographic Province, had a reported range extending from Baja California, Mexico, including the Gulf of California, to Chile (Chirichigno 1974; Robins et al. 1991b). This range consists of tropical and subtropical ocean waters. The recent collection of this species from the warm-temperate waters of southern California represents a latitudinal range extension of over 1000 km.

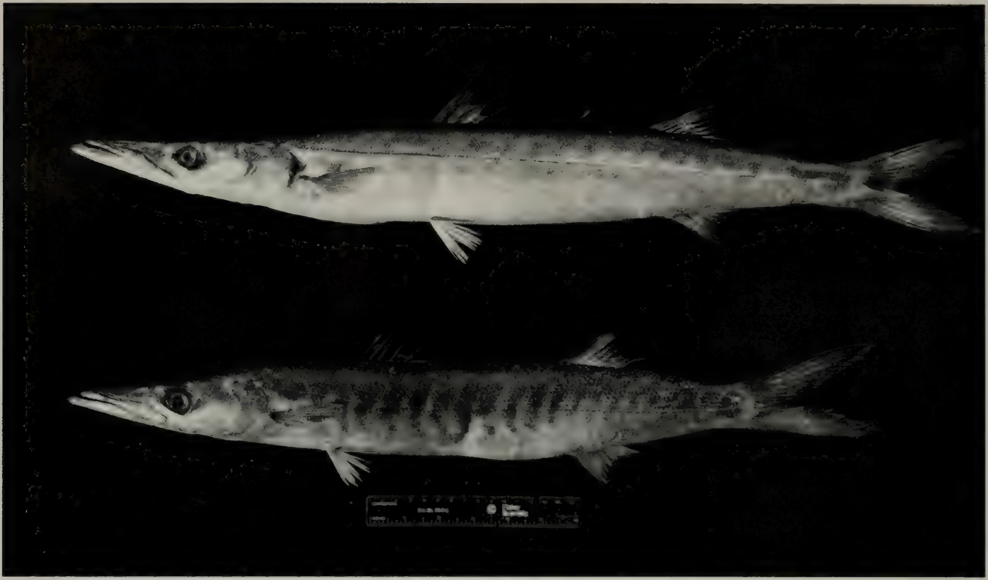


Fig. 1. The upper specimen is a Pacific barracuda, *Sphyraena argentea,* and the lower specimen is the Mexican barracuda, *Sphyraena ensis,* caught off Oceanside (SIO 98-36).

Walford (1937) and Sommer (1995) describe several characteristics that can be used to distinguish the Mexican barracuda from the more common Pacific barracuda (Fig. 1). One of the most distinctive characteristics is the attachment of the pelvic fin, which in the Mexican barracuda is underneath or slightly forward of the posterior tip of the pectoral fin. In the Pacific barracuda the pelvic fin is attached posterior of the pectoral fin. The Mexican barracuda also has numerous dark bars or chevrons on its side and the maxillary extends to the fore margin of the eye. The Pacific barracuda lacks dark bars on its side and has a shorter maxillary. Furthermore, the Mexican barracuda has between 105 and 120 lateral line scales, while the Pacific barracuda has from 160 to 170 (Jordan and Evermann 1896; Gilbert and Starks 1904; Meek and Hildebrand 1923).

Sphyrna lewini

Three species of hammerhead sharks (family Sphyrnidae) have been recorded in California waters (Robins et al. 1991a); however, their occurrence is uncommon. In the eastern Pacific, the distribution of hammerhead sharks is generally restricted to tropical latitudes. The scalloped hammerhead, *Sphyrna lewini* (Griffith and Smith 1834), can be distinguished from *S. tiburo* and *S. zygaena,* the other two species that have been reported in California, by the presence of four lobes on the anterior margin of its head (Miller and Lea 1972). The first reported California records of scalloped hammerhead were caught off Santa Barbara on 28 August 1977 (Fusaro and Anderson 1980). However, Hubbs (1948) mentioned that in 1926, an unusually warm water year, many hammerheads (*Sphyrna* sp.) were caught in southern California. Unfortunately there are no records or mention of the species of hammerhead shark caught. Seigel (1985) reported three additional records from California; one of which was a juvenile. The following information provided is for 20 additional records from southern California that were caught before, during, and after the 1997–1998 ENSO event.

In 1996 and 1997 ten scalloped hammerheads were caught in south San Diego Bay by Mike Irey, a commercial mullet fishermen. These specimens were deposited in the SIO collection and were identified and measured (range 63 to 99 cm TL; $\bar{x}=73$) by R. N. Lea. Nine additional specimens, which were caught in gillnets set by the OREHP assessment program, were also collected from south San Diego Bay (latitude 32°37.10′N, longitude 117°06.63′W) between October 1997 and June 1999. These specimens were identified and measured (range 57 to 164 cm TL, $\bar{x}=93$) by the author. Of these nine specimens, two were deposited in the SIO collection (SIO 98-39) and two in the fish collection at San Diego State University (SDSU 98-101).

On all 19 of these specimens, the lower lobe of the caudal fin and the ventral surface of the pectoral fins had black tips. The female:male sex ratio was roughly equal (9:10). In North American waters, male scalloped hammerheads are reported to become sexually mature at about 180 cm TL and females at around 250 cm TL (Castro 1983; Branstetter 1987). Although none of the specimens reported here were examined for sexual maturity, it is presumed that they were all immature since the largest individual, a female, was only 164 cm TL.

Seigel (1985) reported the first California record of a juvenile scalloped hammerhead, caught on 4 October 1984. This specimen, which was 54.5 cm in total length and possessed a mid-ventral umbilical scar, was probably less than one month old. However, the Marine Vertebrates Collection at SIO includes a scalloped hammerhead specimen (SIO 81-152) that is 47.3 cm in total length that was caught by hook and line just north of the SIO pier (latitude 32°52.0′N longitude 117°15.0′W) on 6 November 1981. This specimen also has an umbilical scar and is probably less than one month old. In addition to these two pups, five of the nine specimens caught by the OREHP assessment program had mid-ventral umbilical scars. They were taken on 6 October 1997 and ranged from 56.5 to 63.1 cm TL ($\bar{x}=61.3$ cm) (Fig. 2). The size of scalloped hammerhead pups at parturition is between 38 and 60 cm TL ($\bar{x}<50$ cm) (Clarke 1971; Branstetter 1987; Chen et al. 1988). Clarke (1971) reported growth rates between 0.03 and 0.25 cm day^{-1} for scalloped hammerhead pups tagged in the wild or retained in laboratory ponds. Based on the presence of their umbilical scars and values reported in the literature, the ages of the 5 pups caught in San Diego Bay were probably between 45 and 94 days old.

The thermal effluent discharged from an electrical generating station at the southern end of San Diego Bay creates a thermal plume that has been reported to elevate water temperatures in this area (Chambers and Chambers 1973; Ford and Chambers 1974). The extent of this thermal plume changes markedly on a seasonal and tidal basis. This area of the bay is also more estuarine than the central and outer portions of San Diego Bay. The area is characterized by higher salinities and elevated water temperatures caused by shallow water depths (<3 m), bottom sediments that are either black or dark gray silty mud which enhance solar absorption, and poor tidal flushing. Seasonal water temperatures in south San Diego Bay range from 14 to 24°C outside the thermal effluent plume, while those influenced by the plume range from 16 to 31°C (Ford and Chambers 1974). Water temperatures in the location where the five pups were collected were around

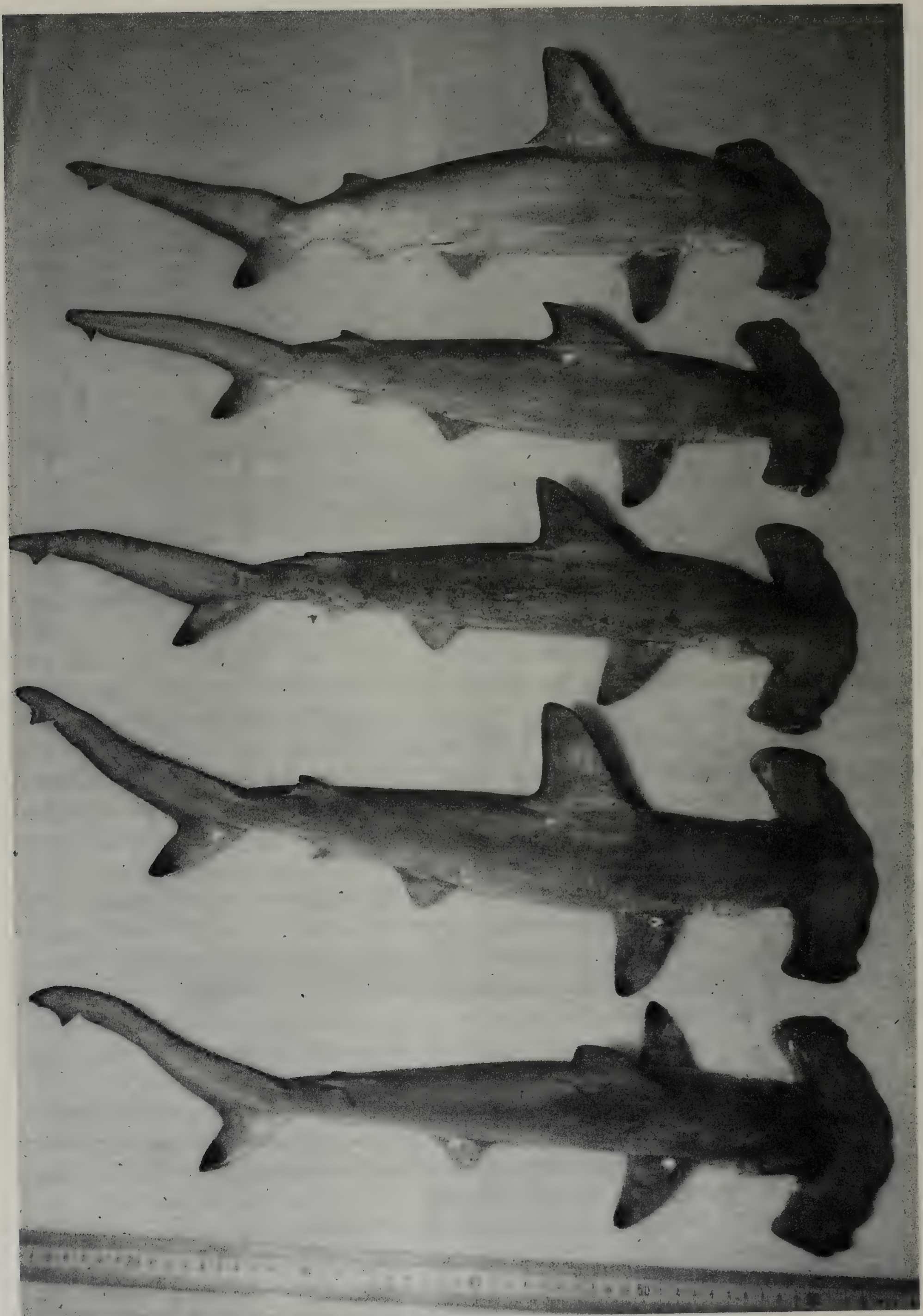


Fig. 2. The three female and two male scalloped hammerhead, *Sphyrna lewini,* pups caught in south San Diego Bay on 6 October 1997.

24°C during Fall 1997. Furthermore, this area of the bay is also very turbid, with average transparencies of <2.0 m (Chambers and Chambers 1973; M. Shane unpub. data).

The physical environmental conditions that exist in south San Diego Bay are similar to those in Kanahoe Bay, Oahu, Hawaii, which is a known pupping ground for scalloped hammerheads (Clarke 1971; Holland et al. 1993). Because of the number of juvenile specimens captured in the southern end of San Diego Bay, before, during, and after the 1997-98 ENSO, this area may function as both a pupping ground and warm water refugium for scalloped hammerheads that travel north during warm water years.

Acknowledgments

The collection of these valuable specimens was made possible through funding by the California Department of Fish and Game's Ocean Resources Enhancement and Hatchery Program administered by S. Crooke. I am especially thankful to G. Stutzer for assisting with the OREHP assessment efforts and for first observing the unfamiliar barracuda caught off Oceanside; S. Aalbers for bringing to my attention his underwater photograph of the school of barracuda; H. J. Walker for providing access to the specimens in the fish collection at SIO; R. N. Lea for providing his data on *S. lewini* and his review of the manuscript; and for the critical reviews of R. F. Ford, C. G. Lowe and R. H. Rosenblatt.

Literature Cited

Branstetter, S. 1987. Age, growth and reproductive biology of the silky shark, *Carcharhinus falciformis,* and the scalloped hammerhead, *Sphyrna lewini,* from the northwestern Gulf of Mexico. Environ. Biol. Fish., 19(3):161–173.

Brooks, A. J. 1987. Two species of Kyphosidae seen in King Harbor, Redondo Beach, California. Calif. Fish and Game, 17(1):49–50.

Castro, J. I. 1983. The sharks of North American waters. Texas A&M University Press, 180 pp.

Chambers, R. W. and R. L. Chambers. 1973. Thermal distribution and biological studies for the south bay power plant. Final report. Volume 4A-B thermal measurements May 1973. Environmental Engineering Laboratory Tech. Report on purchase order #P-25072 for San Diego Gas and Electric Company, iii + 177 pp.

Chen, C. T., T. C. Leu and S. J. Joung. 1988. Notes on reproduction in the scalloped hammerhead, *Sphyrna lewini,* in northeastern Taiwan waters. Fish. Bull., 86(2):389–393.

Chirichigno, N. F. 1974. Clave para identificar los peces marinos del Peru. Inf. Inst. Mar Peru, 44: 387 pp.

Clarke, T. A. 1971. The ecology of scalloped hammerhead shark, *Sphyrna lewini,* in Hawaii. Pac. Sci., 25:133–144.

Ford, R. F. and R. L. Chambers. 1974. Thermal distribution and biological studies for the south bay power plant. Final report. Volume 5C biological studies September 1972-August 1973. Environmental Engineering Laboratory Tech. Report on purchase order #P-25072 for San Diego Gas and Electric Company, vii + 189 pp.

Fusaro, C. and S. Anderson. 1980. First California record: The scalloped hammerhead shark, *Sphyrna lewini,* in coastal Santa Barbara waters. Calif. Fish and Game, 66(2):121–123.

Gilbert, C. H. and E. C. Starks. 1904. The fishes of Panama Bay. California Academy of Sciences, Memoirs vol. 4; reprinted in Hopkins Seaside Laboratory of Leland Stanford, Jr., Contributions to Biology, 32:62–63.

Griffith, E. and C. H. Smith. 1834. The class Pisces, arranged by the Baron Cuvier, with supplementary additions, by Edward Griffith, F.R.S., &c. and Lieut.-Col Charles Hamilton Smith, F.R., L.S.S., &c. &c. London. Class Pisces, Cuvier 1–680.

Holland, K. N., B. M. Wetherbee, J. D. Peterson and C. G. Lowe. 1993. Movements and distribution of hammerhead shark pups on their natal grounds. Copeia, 1993(2):495–502.

Hubbs, C. L. 1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. J. Mar. Res., 7(3):459–482.

Hubbs, C. L. and L. P. Schultz. 1929. The northward occurrence of southern forms of marine life along the Pacific coast in 1926. Calif. Fish and Game, 15(3):234–241.

Jordan, D. S. and B. W. Evermann. 1896. The fishes of North and Middle America. Bull. U.S. Nat. Mus., 47(1):822–826.

Jordan, D. S. and C. H. Gilbert. 1882. List of fishes collected at Mazatlan, Mexico, by Charles H. Gilbert. Bull. U. S. Fish Comm., v. 2 [1882]:105–108.

Lea, R. N. and R. H. Rosenblatt. 1992. The Cortez grunt (*Haemulon flaviguttatum*) recorded from two embayments in southern California. Calif. Fish and Game, 78(4):163–165.

Lea, R. N. and H. J. Walker, Jr. 1995. Record of the bigeye trevally, *Caranx sexfasciatus,* and Mexican lookdown, *Selene brevoorti,* with notes on other carangids from California. Calif. Fish and Game, 81(3):89–95.

Meek, S. E. and S. F. Hildebrand. 1923. The marine fishes of Panama. Field Museum of Natural History, Publ. 215, 15(1):282–288.

Miller, D. J. and R. N. Lea. 1972. Guide to the coastal marine fishes of California. California Department of Fish and Game, Fish Bulletin 157, 235 pp.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea and W. B. Scott. 1991a. Common and scientific names of fishes from the United States and Canada, fifth edition. American Fisheries Society Special Publication 20, 183 pp.

———. 1991b. World fishes important to North Americans exclusive of species from the continental waters of the United States and Canada. American Fisheries Special Publication 21, 243 pp.

Seigel, J. A. 1985. The scalloped hammerhead, *Sphyrna lewini,* in coastal southern California waters: Three records including the first reported juvenile. Calif. Fish and Game, 71(3):189–190.

Sommer, C. 1995. Sphyraenidae. *in* Guia FAO para identification de especies para los fines de la pesca. Pacifico Centro-Oriental. (W. Fischer, F. Krupp, W. Schneider, C. Sommer, K. E. Carpenter, and V. Niem, eds.), Vol. III:1618–1621.

Walford, L. A. 1931. Northward occurrence of southern fish off San Pedro in 1931. Calif. Fish and Game, 17(4):401–405.

———. 1937. Marine game fishes of the Pacific coast from Alaska to the equator. University of California Press, 205 pp. + 69 plates.

Accepted for publication 22 December 2000.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 167–169

Occurrence of the Loosetooth Parrotfish, *Nicholsina denticulata* (Scaridae), from Santa Catalina Island, California

Robert N. Lea,[1] Erik D. Erikson,[2] Kelly Boyle,[3] and Robert Given[4]

[1]*California Department of Fish and Game, Marine Region, 20 Lower Ragsdale Drive, Monterey, CA 93940*
[2]*MetaVisual, Inc., PO Box 592, Carmel, CA 93921*
[3]*Department of Biological Science, California State University at Fullerton, Fullerton, CA 92834*
[4]*Marymount College, Rancho Palos Verdes, CA 90275*

The parrotfishes, family Scaridae, are characterized as specialized perciform fishes that closely associate with reefs and are primarily tropical in distribution (Schultz 1958, 1969 and Nelson 1994). Rosenblatt and Hobson (1969) revised the systematics of eastern Pacific parrotfishes, recognizing three genera comprising six species. *Scarus* is considered the typical parrotfish genus, with four species in the eastern Pacific. *Nicholsina,* the more primitive (or plesiomorphic) genus, is monotypic in the eastern Pacific. *Calotomus,* the third genus, is Indo-Pacific in origin and rare in the eastern Pacific. *Nicholsina denticulata* (Evermann & Radcliffe, 1917), the loosetooth parrotfish, is a smaller, less colorful species compared to the members of the genus *Scarus* occupying the Panamic Region.

The distribution of *Nicholsina denticulata* is listed by Thomson et al. (2000) as, " . . . throughout the Gulf [of California] and from Bahía Magdalena south to Peru and the Islas Galápagos." We are aware of two collections, representing 19 specimens, from Bahía Santa Maria (Scripps Institution of Oceanography, Marine Vertebrates Collection, SIO 64-42 and 64-43). Bahía Santa Maria is approximately 20 kilometers north of the entrance to Magdalena Bay, on the outer coast of Baja California Sur. While surveying fishes of the Islas San Benito, Baja California, Mexico (ca. lat 28°18′N), located 110 km off the coast of central Baja California and 25 km west of the seaward side of Isla Cedros, divers (R. N. Lea, R. E. Snodgrass, and D. V. Richards) observed *Nicholsina denticulata* during several scuba dives in August 1996 and again on four dives in August 1998. *Nicholsina* had not been noted at Islas San Benito on six previous trips by RNL (since 1984), and there are no known collections of the species from the outer coast of Baja California north of Bahía Santa Maria. During the Islas San Benito expedition of 2–6 August 1998, we observed loosetooth parrotfish in relatively shallow water (8 to 12 m) and often in association with the alga *Eisenia;* sea surface temperatures at the islands ranged from 19.1° to 20.9° C. In the Sea of Cortez, *Nicholsina* "is often observed among *Sargassum, Padina,* and other algae . . ." (Thomson et al. 2000).

On 22 May 1999, E. Erikson while diving at 6 m at Lovers Cove Reserve, Santa Catalina Island (lat 33°20.6′N, long 118°19.1′W), noticed a fish swimming in *Eisenia* with which he was not familiar. One month later on 20 June Erikson was able to photograph this unidentified species. The photograph was sent to R. Given and then to R. N. Lea for identification. The fish was recognized as the

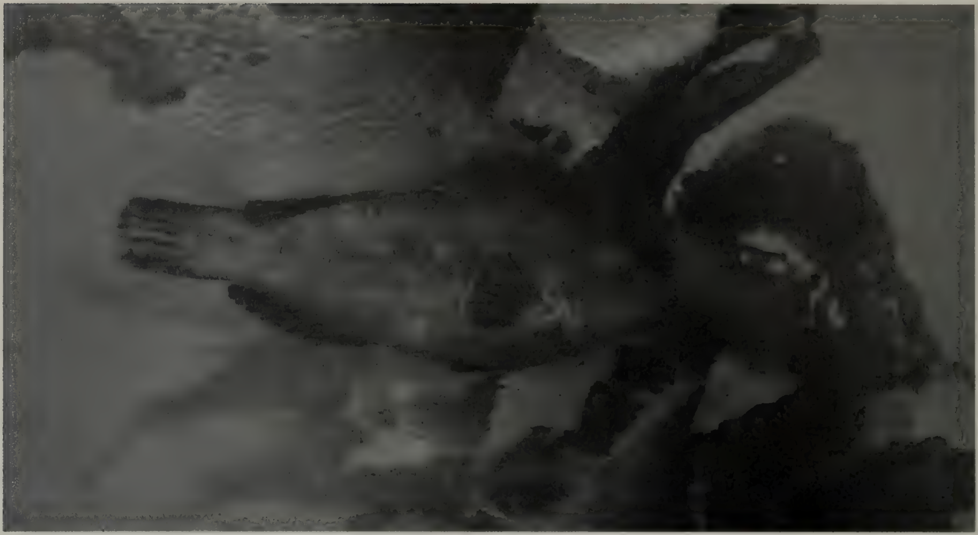


Fig. 1. Loosetooth parrotfish from Casino Point Underwater Park, Santa Catalina Island, 12 September 1999. Photograph by E. Erikson.

loosetooth parrotfish based on its general body morphology, large scalation, and rather drab brownish-green coloration (Fig. 1). The coloration of *Nicholsina* is characterized by Thomson et al. (2000) as " . . . variable, usually reddish to drab brown or greenish with diffuse dark mottling matching its surroundings." Characteristics separating the various parrotfish genera are primarily based on structure of the teeth and patterns of scalation (requiring close or in-hand examination). The photograph is typical of the species.

These observations and photographic documentation represent the first record of the species, as well as the family, from Californian waters. Following the 22 May sighting, loosetooth parrotfish were observed at Santa Catalina Island, at Lovers Cove Reserve and Casino Point Underwater Park, by EE on four other occasions in 1999: 27 May at 6 m, 16.1°C (temperature is at depth of sighting); 20 June at 6 m, 16.7°C; 12 September at 7.5 to 9 m, 17.2°C; and 23 September at 4.5 m, 16.7°C. On the 12 September dive two parrotfish, which appeared to be a male and female pair, were observed and photographed over a 45-minute period. The estimated size for these fish was between 20 to 24 cm total length. Kelly Boyle also observed loosetooth parrotfish in September 1999 at Santa Catalina Island, Casino Point Underwater Park. On 11 September, a single loosetooth parrotfish was noted swimming at 10 m depth. On 17 September, KB with three other divers observed a single parrotfish on three separate dives that they assumed to be the same individual. The sightings were between 4.5 and 10.5 m depth and the fish was estimated as 25 cm total length; it was grazing on the alga *Sargassum palmeri.*

The 1996 and 1998 observations at Islas San Benito are, to our knowledge, the first records of the species north of Bahía Santa Maria. Magdalena Bay is considered the northern boundary of the Panamic Biogeographic Province; Bahía Santa Maria is essentially a northern extension of Magdalena Bay. Oceanographically, 1992 through 1996 was a period of exceptionally warm water in the eastern

North Pacific Ocean. Commencing in mid-1997, ocean temperatures for this region became more extreme and were manifested as the 1997–98 El Niño event, with the highest recorded sea-surface temperatures for outer Baja California and southern California during the 20th century (Lea and Rosenblatt 2000). The observations of loosetooth parrotfish during the colder La Niña period of 1999 are, in our opinion, the result of fish that most likely arrived during the 1997–98 El Niño and remained unnoticed until the observations discussed in this paper were made.

Acknowledgments

We would like to thank William Mercadante who aided E. Erikson in his observations at Santa Catalina Island. We also acknowledge Michael Horn, Camm Swift, and two anonymous reviewers for their constructive comments regarding this paper.

Literature Cited

Evermann, B. W. and L. Radcliffe. 1917. The fishes of the west coast of Peru and the Titicaca Basin. Bull. U. S. Nat. Mus., 95:1–166.

Lea, R. N. and R. H. Rosenblatt. 2000. Observations on fishes associated with the 1997–98 El Niño off California. CalCOFI Reports, 41:117–129.

Nelson, J. S. 1994. Fishes of the world. 3rd edition. John Wiley & Sons, Inc. New York. 600 pp.

Rosenblatt, R. H. and E. S. Hobson. 1969. Parrotfishes (Scaridae) of the eastern Pacific, with a generic rearrangement of the Scarinae. Copeia 1969(3):434–453.

Schultz, L. P. 1958. Review of the parrotfishes Family Scaridae. Bull. U. S. Nat. Mus., 214:1–143.

Schultz, L. P. 1969. Taxonomic status of the controversial genera and species of parrotfishes, with descriptive list (family Scaridae). Smithsonian Contrib. Zool. No. 17. 49 pp.

Thomson, D. A., L. T. Findley, and A. N. Kerstitch. 2000. Reef fishes of the Sea of Cortez: the rocky-shore fishes of the Gulf of California, revised edition. The Univ. of Texas Press, Austin. 353 pp.

Accepted for publication 21 December 2000.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 170–174

Increase in Occurrence and Abundance of Zebraperch (*Hermosilla azurea*) in the Southern California Bight in Recent Decades

Erick A. Sturm[1] and Michael H. Horn

Department of Biological Science, California State University, Fullerton
Fullerton, California 92834-6850

The zebraperch, *Hermosilla azurea* Jenkins and Evermann 1889, a warm-temperate member of the widespread but mainly tropical perciform family Kyphosidae, occurs in coastal waters of southern California and Baja California and in the Gulf of California (Jenkins and Evermann 1889; Miller and Lea 1972; Eschmeyer et al. 1983; de la Cruz-Aguero et al. 1994; Rodriguez-Romero et al. 1994; Thomson et al. 2000). The northerly range limit of this species was given as Monterey Bay (36° 36′ N) by Miller and Lea (1972) and Eschmeyer et al. (1983), but the species has been regarded as uncommon in California (Miller and Lea 1972) and rare north of southern California (Eschmeyer et al. 1983). In the mid-1980s, zebraperch were captured in the Klamath River estuary in northern California (41° 31′ N) to establish the northernmost range limit for the species (Fritzsche et al. 1991). In this note, we provide evidence that the northerly range extensions recorded for the zebraperch in recent decades correspond to short-term periods of ocean warming associated with El Niño conditions. We also offer support for the hypothesis that this fish has increased in abundance and established breeding populations in the Southern California Bight over the past 15–20 years coincident with a sustained warming trend in the region over the same time period.

The zebraperch apparently was noted as a member of the California ichthyofauna during the middle years of the last century, at least according to published records. The fish was first reported in the Southern California Bight in waters off San Diego County by Hubbs (1948) who noted that the fish began occurring in this area during a warm-water event. Lockley (1952) captured juveniles in tidepools at La Jolla, California, in the mid 1940s and, since that time, the species has been recorded as present in the San Diego area (Limbaugh 1955; Quast 1968; Barry and Ehret 1993).

The occurrence of the zebraperch in more northerly areas of the Southern California Bight and north of Point Conception (34° 30′ N) appears to be linked to short-term periods of ocean warming associated with El Niño conditions and to the sustained period of warming that occurred over the last two decades up to 1998 (Table 1). Northerly range extensions of the species to Monterey Bay in 1964 (Phillips 1965) and to the Klamath River estuary in 1985 and 1987–1988 (Fritzsche et al. 1991) followed the respective El Niño events of 1963 and 1982–1983. Records of zebraperch at King Harbor in Redondo Beach (Pondella 1997) and at Santa Cruz Island (Feder et al. 1974) in the early 1970s followed the 1972–

---

[1] Current address: National Marine Fisheries Service, Hatfield Marine Science Center, Newport, Oregon 97365.

Table 1. Year and location where zebraperch, *Hermosilla azurea,* were sighted or captured in California waters north of La Jolla* and the year of the El Niño event preceding the sighting or capture.

Year of sighting or capture	Sighted (S) or Captured (C)	Location	Year of El Niño event	Reference
1964	C	Carlsbad 33°05′ N, 117°18′ W	1963	Marine Vertebrates Collection, Scripps Institution of Oceanography (SIO 64–92)
1964	C	Monterey Bay 36°36′ N, 121°53′ W	1963	Phillips (1965)
1965	C	Oxnard 34°09′ N, 119°12′ W	1963	Fitch (1966)
early 1970s	S	Santa Cruz Island 34°01′ N, 119°41′ W	1972–1973	Feder et al. (1974)**
1974–2001	S	King Harbor, Redondo Beach 33°50′ N, 118°23′ W	1972–1973, 1982–1983, 1991–1992 & 1997–1998	Pondella (1997) D. Pondella, pers. comm.
1976, 1978 & 1979	S	Santa Catalina Island 33°26′ N, 118°30′ W	1972–1973	DeMartini and Coyer (1981)
1985, 1987 & 1988	C	Klamath River Estuary 41°31′ N, 124°05′ W	1982–1983	Fritzsche et al. (1991)
1990 & 1996	S	Santa Barbara Island 33°29′ N, 119°02′ W	1991–1992	D. Richards, pers. comm.
1996	S	Santa Barbara 34°25′ N, 119°41′ W	1991–1992	S. Anderson, pers. comm.
1996	C	San Clemente Island 33°00′ N, 118°33′ W	1991–1992	Sturm and Horn, current paper
1997–1998	S&C	Gaviota Pier, Santa Barbara 34°28′ N, 120°13′ W	1997–1998	D. Kushner, pers. comm.
1998–1999	S	Coal Oil Point, Santa Barbara 34°25′ N, 119°41′ W	1997–1998	D. Kushner, pers. comm.

* The Marine Vertebrates Collection at Scripps Institution of Oceanography also has 18 records containing *H. azurea* captured or observed in the La Jolla area with dates ranging from 1939 to 1969.

** This paper did not list the year when zebraperch were sighted at Santa Cruz Island.

1973 El Niño warming interval. Sightings or captures of zebraperch in the Santa Barbara area and in the Channel Islands in the 1990s also seem to correspond to El Niño events (Table 1) that were closely spaced in time and part of a sustained ocean warming trend during most of this decade (Smith 1995; Bograd et al. 2000). The aggregations of zebraperch, estimated in some cases at >100 individuals (D. Kushner, pers. comm.), seen in the Santa Barbara area in 1997, 1998 and 1999 are indications of an abundant and established population.

Further documentation of the responsiveness of the zebraperch to warmer temperatures and of its expanded distribution in southern California comes from observations spanning key time intervals at specific locations. Zebraperch were commonly observed in the warm-water effluent of the Pacific Gas and Electric

(PG&E) steam-generating plant at Morro Bay north of Point Conception (Feder et al. 1974), apparently in the 1950s and 1960s. By the 1980s, however, the fish had disappeared from this otherwise cool-temperature locality based on interviews conducted by one of us (MHH in the late 1980s) with PG&E personnel and biologists at the California Department of Fish and Game office in Morro Bay. In contrast, the species has inhabited King Harbor in southern California consistently since 1974 (Pondella 1997; D. Pondella, pers. comm.). King Harbor has become a haven for warm-water fishes because of the elevated temperatures of the water discharged into the harbor by the Southern California Edison Redondo Beach Generating Station and because of its protective breakwaters (Stephens and Zerba 1981; Brooks 1987; Pondella 1997; Pondella et al. 1998). At San Clemente Island, Santa Catalina Island and upper Newport Bay, zebraperch were captured in recent years but not in earlier years even though in some cases similar collecting methods were used. In a gill net survey of the near-shore fish community at Wilson Cove, San Clemente Island, Horn (1977) collected no zebraperch in 1975 or 1976, whereas we captured nine zebraperch (mean length 184.8 mm SL; range 170–195 mm) at this location in October 1996 using the same gear in a one-hour set (unpublished data). Hobson et al. (1981) did not list zebraperch as one of the major near-shore fishes at Santa Catalina Island; however, beginning in the mid-1980s, zebraperch have been seen repeatedly at several shallow-water localities around the island (J. Cvitanovich, pers. comm.). Moreover, on numerous occasions from 1993 through 1998, we observed young-of-the-year fish (<75 mm SL) and collected large juvenile and adult fish (>200 mm SL) with spear gun and gill net at various inshore (<5 m) sites at the island (Sturm and Horn 1998; unpublished data). In an extensive multiple-gear sampling program conducted in upper Newport Bay in the late 1970s, Horn and Allen (1985) collected no zebraperch. However, in the mid-1980s (Allen 1988) and throughout most of the 1990s (California Department of Fish and Game Bay-Estuary Near-Shore Ecosystem Survey [BENES], unpublished data; L. Allen, pers. comm.), zebraperch were captured routinely at gill net stations in the upper and lower bay. Finally, studies involving the distribution of zebraperch larvae reveal little about the response of the fish to temperature change except that the larvae occur in shallow, near-shore waters and have been identified only from samples taken south of Point Conception—at the San Onofre Nuclear Generation Station (33°22′ N) by Walker et al. (1987) from 1978–1980 surveys and in Santa Monica Bay (34°00′ N) by Stevens et al. (1989) from 1978 and 1981 CalCOFI surveys.

Taken together, the available literature and unpublished observations, including our own, indicate that the zebraperch responded differently to the short-term El Niño conditions of recent decades than to the sustained warming trend in the Southern California Bight that began in 1977 and extended through to 1994 (Smith 1995) and beyond, culminating in a strong El Niño event in 1997–1998 (Lea and Rosenblatt 2000) and ending with a La Niña condition in 1998–1999 (Bograd et al. 2000). The zebraperch appeared to extend its range northward following an El Niño event and then fail to establish a resident population in the new northern locality, in particular, Morro Bay, Monterey Bay or the Klamath River estuary. This record of extension and retreat is a common pattern that has been documented for other coastal fishes with warm-water affinities (e.g. Hubbs 1948; Radovich 1961; Norris 1963; Fitch 1966; Bond 1985). On the other hand, under the persistent warming regime of the last two decades, the zebraperch appears to have established itself widely as a resident, breeding species in the Southern California Bight. The records and observations of recent years cited above provide support for this contention. Whether the zebraperch will persist as an established population in the Southern California Bight remains to be seen, but sightings of the species in 1999 at Santa Barbara (Table 1), in May 2000 at Santa Catalina Island (J. Cvitanovich, pers. comm.) and in September 2000 at Laguna Beach (K. Boyle, pers. comm.), all following a cool La Niña period, suggest that it will continue to be a part of the ichthyofauna of the region.

Acknowledgments

We thank L. Allen, S. Anderson, D. Kushner, D. Pondella, D. Richards and C. Valle for supplying specimens or unpublished records of zebraperch captures and sightings. The gill net study we conducted at San Clemente Island in October 1996 would not have been possible without the help of T. Gibson, S. Heid, A. Lowe, E. Lowe, S. Murray and O. Rivas. We are grateful to R. Lea for his valuable comments on an earlier version of the manuscript.

Literature Cited

Allen, L.G. 1988. Results of a two-year monitoring study on the fish populations in the restored, uppermost portion of Newport Bay, California, with emphasis on the impact of additional estuarine habitat on fisheries-related species. Final Rep., Contract, Nat. Mar. Fish. Serv., NOAA, La Jolla. 87 pp.

Barry, J.P. and M.J. Ehret. 1993. Diet, food preference, and algal availability for fishes and crabs on intertidal reef communities in southern California. Environ. Biol. Fishes, 37:75–95.

Bograd, S.J., P.M. DiGiacomo, R. Durazo, T.L. Hayward, K.D. Hyrenbach, R.J. Lynn, A.W. Mantyla, F.B. Schwing, W.J. Sydeman, T. Baumgartner, B. Lavaniegos, and C.S. Moore. 2000. The state of the California Current: 1999–2000: forward to a new regime? CalCOFI Rep., 41:26–52.

Bond, C.E. 1985. Northward occurrence of the opaleye *Girella nigricans,* and the sharpnose seaperch, *Phanerodon atripes.* Calif. Fish & Game, 71:56-57.

Brooks, A.J. 1987. Two species of Kyphosidae seen in King Harbor, Redondo Beach, California. Calif. Fish & Game, 73:49-50.

De la Cruz-Aguero, J., F. Galván-Magaña, L.A. Abitia-Cárdenas, J. Rodríguez-Romero, and F.J. Gutiérrez-Sánchez. 1994. Systematic list of marine fishes from Bahia Magdalena, Baja California Sur (Mexico). Ciencas Marinas, 20:17-31.

DeMartini, E.E. and Coyer, J.A. 1981. Cleaning and scale eating in juveniles of the kyphosid fishes, *Hermosilla azurea* and *Girella nigricans.* Copeia, 1981:785-789.

Eschmeyer, W.N., E.S. Herald, and H. Hammann. 1983. A field guide to Pacific Coast fishes of North America. Peterson Field Guide Series. Houghton Mifflin Company, xiv + 336 pp.

Feder, H.M., C.H. Turner, and C. Limbaugh. 1974. Observations on fishes associated with kelp beds in southern California. Calif. Dept. Fish & Game, Fish Bull. 160. 144 pp.

Fitch, J.E. 1966. A marine catfish, *Bagre panamensis* (Gill), added to the fauna of California, and other anomalous fish occurrences off southern California in 1965. Calif. Fish & Game, 52:214-215.

Fritzsche, R., G. Aasen, L. Everest, P. Petros, and S. Shimek. 1991. Northern range extension for the zebraperch (*Hermosilla azurea,* Jenkins and Evermann). Calif. Fish & Game, 77:106–107.

Hobson, E.S., W.N. McFarland and J.R. Chess. 1981. Crepuscular and nocturnal activities of Californian nearshore fishes, with consideration of their scotopic visual pigments and the photic environment. Fish. Bull., 79: 1-30.

Horn, M.H. 1977. Abundance and species composition of fishes. Pp. 41-46 *in* Influence of domestic wastes on the structure and energetics of intertidal communities near Wilson Cove, San Clemente Island (M. M. Littler and S. N. Murray, eds.), Calif. Water Resources Ctr., Contract No. 164.

Horn, M.H. and L.G. Allen. 1985. Fish community ecology in southern California bays and estuaries. Pp. 169–170 *in* Fish community ecology in estuaries and coastal lagoons, towards an ecosystem integration (A. Yañez-Arancibia, ed.). UNAM Press, Mexico.

Hubbs, C.L. 1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. J. Mar. Res., 7:459-482.

Jenkins, O.P. and B.W. Evermann. 1889. Description of eighteen new species of fishes from the Gulf of California. Proc. U. S. Nat. Mus., pp. 137-158.

Lea, R.N. and R.H. Rosenblatt. 2000. Observations on fishes associated with the 1997–98 El Niño off California. CalCOFI Rep., 41:117-129.

Limbaugh, C. 1955. Fish life in the kelp beds and the effects of kelp harvesting. Univ. Calif. Inst. Mar. Res., IMR Ref. No. 55-9. 158 pp.

Lockley, A.S. 1952. Description of the young of the kyphosid fish, *Hermosilla azurea,* from California. Copeia, 1952:42.

Miller, D.J. and R.N. Lea. 1972. Guide to the coastal marine fishes of California. Calif. Dept. Fish & Game, Fish Bull. 157. 249 pp.

Norris, K.S. 1963. The functions of temperature in the ecology of the percoid fish *Girella nigricans* (Ayres). Ecol. Monogr., 33:23-62.

Phillips, J.B. 1965. Northern range extension for the zebraperch, *Hermosilla azurea* Jenkins and Evermann. Calif. Fish & Game, 51:55-56.

Pondella, D.J. 1997. The first occurrence of the Panamic sergeant major, *Abudefduf troschelii* (Pomacentridae), in California. Calif. Fish & Game, 83:84-86.

Pondella, D.J. R. Snodgrass, M.T. Craig, and H. Khim. 1998. Re-occurrence of the threebanded butterflyfish, *Chaetodon humeralis* (Chaetodontidae), with notes on its distribution in Southern California. Bull. So. Calif. Acad. Sci., 97:121-124.

Quast, J.C. 1968. Observations on the food of the kelp-bed fishes. Pp. 109–142 *in* Utilization of kelp-bed resources in southern California (W.J. North and C.L. Hubbs, eds.). Calif. Dept. Fish & Game, Fish. Bull. 139.

Radovich, J. 1961. Relationships of some marine organisms of the Northeast Pacific to water temperatures. Calif. Dept. Fish & Game, Fish Bull. 112. 62 pp.

Rodríguez-Romero, J., L.A. Abitia-Cárdenas, F. Galván-Magaña, and H. Chávez-Ramos. 1994. Composition, abundance and specific richness of fishes from Concepcion Bay, Baja California Sur, Mexico. Ciencias Marinas, 20:321-350.

Smith, P.E. 1995. A warm decade in the Southern California Bight. CalCOFI Rep., 36:120-126.

Stephens, J.S., Jr. and K. Zerba. 1981. Factors affecting fish diversity on a temperate reef. Environ. Biol. Fishes, 6:111-121.

Stevens, E.G., W. Watson, and H.G. Moser. 1989. Development and distribution of larvae and pelagic juveniles of three kyphosid fishes (*Girella nigricans, Medialuna californiensis,* and *Hermosilla azurea*) off California and Baja California. Fish. Bull., 87:745-768.

Sturm, E.A. and M.H. Horn. 1998. Food habits, gut morphology and pH, and assimilation efficiency of the zebraperch *Hermosilla azurea,* an herbivorous kyphosid fish of temperate marine waters. Mar. Biol., 132:515-522.

Thomson, D.A., L.T. Findley, and A. N. Kerstitch. 2000. Reef fishes of the Sea of Cortez: the rocky-shore fishes of the Gulf of California. Rev. edition. Univ. Texas Press, xx + 353 pp.

Walker, H.J., W. Watson, and A.M. Barnett. 1987. Seasonal occurrence of larval fishes in the nearshore Southern California Bight off San Onofre, California. Estuar. Coast. Shelf Sci., 25:91-109.

Accepted for publication 29 January 2001.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 175–185

New and Unusual Reef Fish Discovered at the California Channel Islands During the 1997–1998 El Niño

Daniel V. Richards[1] and John M. Engle[2]

[1]*Channel Islands National Park, 1901 Spinnaker Drive, Ventura, California, 93001, Phone: 805-658-5760 Fax: 805-658-5798 Email: dan_richards@nps.gov*
[2]*Tatman Foundation and Marine Science Institute, University of California, Santa Barbara, California 93106*

Abstract.—Observations of warm-water species rarely seen in California are often associated with El Niño Southern Oscillations (ENSO). Here we document new occurrences of tropical reef fish at the California Channel Islands. In 1998, three species, new to California were recorded at San Clemente or Santa Catalina islands (*Apogon pacificus, Nicholsina denticulata,* and *Chromis alta*). New island records of six tropical species (*Azurina hirundo, Apogon guadalupensis, Scorpaenodes xyris, Chaenopsis alepidota, Chaetodon falcifer,* and *Chilomycterus reticulatus*) from the northern Channel Islands extend the northern range of these species. Several of these species seem well established and appeared to be reproductive. Others diminished during the cold water period in 1999.

The California Channel Islands are bathed in the mix of currents of the southern California Bight, creating a transition zone with cold temperate waters around San Miguel and Santa Rosa islands in the northwest to warm temperate water around Santa Catalina and San Clemente islands in the southeast (Fig. 1). The location of the islands within this transition zone creates a shift from a northern species assemblage to a southern species assemblage over a relatively short distance (Cross and Allen 1993; Engle 1993).

The 1997–1998 El Niño was one of the strongest on record with some of the highest temperature anomalies ever recorded (McPhaden 1999). Above normal sea temperatures defined the El Niño from May 1997 to August 1998 (NOAA CoastWatch Bulletins). The peak sea-surface temperatures of 1998 capped almost a decade of above average temperatures in Southern California and the Eastern Pacific. Late 1998 and 1999 saw a reverse of the warm conditions as La Niña conditions prevailed.

With the warm waters of El Niño we saw a number of tropical and subtropical species at the islands. Engle and Richards (2001) report new and unusual invertebrate sightings in a companion paper. The fish sightings we report here include tropical species seen for the first time at the islands and southern species that appear to be establishing themselves farther north at the colder islands. Large El Niño events can almost be tracked by following new records of tropical fishes and invertebrates reported in the literature. Increased sightings followed El Niño events around 1959 (Radovich 1961; Strachen et al. 1968), 1983 (Lea and Vojkovich 1985; Lea and Rosenblatt 1992), 1992, (Lea and McAlary 1994) and now 1998 (this volume; Lea and Rosenblatt 2000).

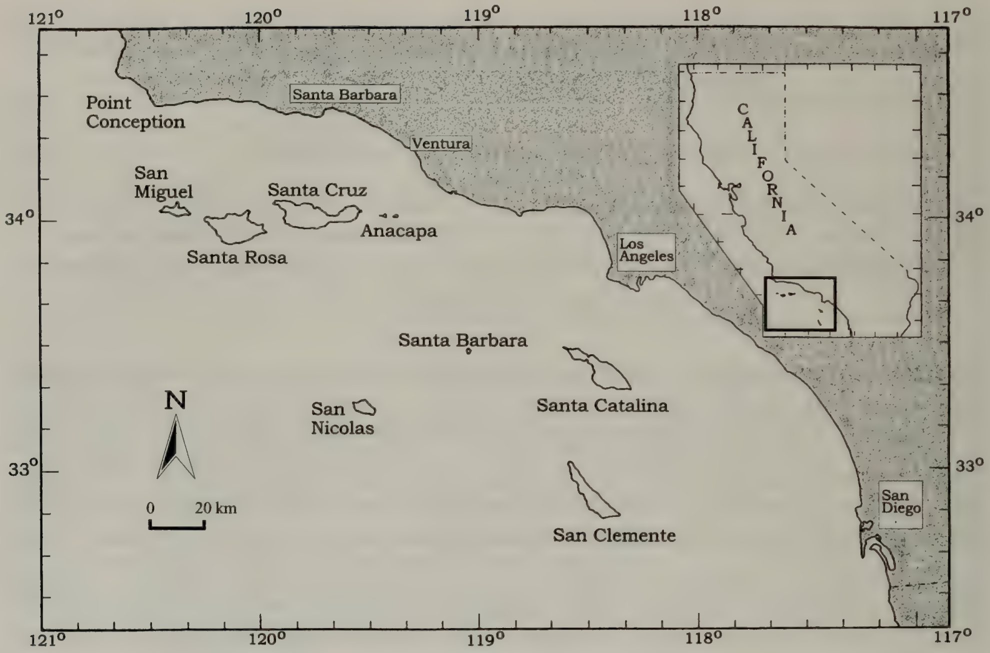

121°
120°
119°
118°
117°
34°
33°
Point Conception
Santa Barbara
Ventura
San Miguel
Santa Cruz
Anacapa
Santa Rosa
Los Angeles
CALIFORNIA
Santa Barbara
Santa Catalina
San Nicolas
N
0
20 km
San Clemente
San Diego

Fig. 1. The California Channel Islands.

Methods

The eight Channel Islands off the southern California coast have been surveyed annually since 1980 in cooperative studies by the Channel Islands National Park (CINP) kelp forest monitoring program or the Channel Islands Research Program (CIRP) through support from the Tatman Foundation. CINP divers regularly monitor 16 fixed sites as part of the kelp forest monitoring program and population dynamics of invertebrate, algal, and fish species are measured. Fishes are quantified in visual transects and Roving Diver Fish Counts twice each year on different dates (Davis et al. 1999). CIRP divers use Roving Dive Fish Counts, general surveys and species lists at a broader spectrum of sites to provide an overview of the island ecosystems. Both programs use a general search method to note species in the field, often with several divers contributing. Unusual fishes were observed by multiple divers and photographed whenever possible. Collections were not made. Roving diver fish counts were developed as a standard means of quantifying relative abundance of fish species.

New Species Records for the California Channel Islands

Family Apogonidae

Apogon pacificus (Herre 1935), pink cardinalfish

Previous reported range.—Islas San Benito to Peru (Thomson et al. 1987). La Jolla Canyon, California (Lea and Rosenblatt 2000).

Remarks.—A single pink cardinalfish, *Apogon pacificus,* was observed and photographed (R. Herrmann, D. Richards) (Fig. 2) on 13 September 1998 in Bat Ray Cove on the southeast tip of San Clemente Island (32°49.27′ N, 118° 21.03′ W).

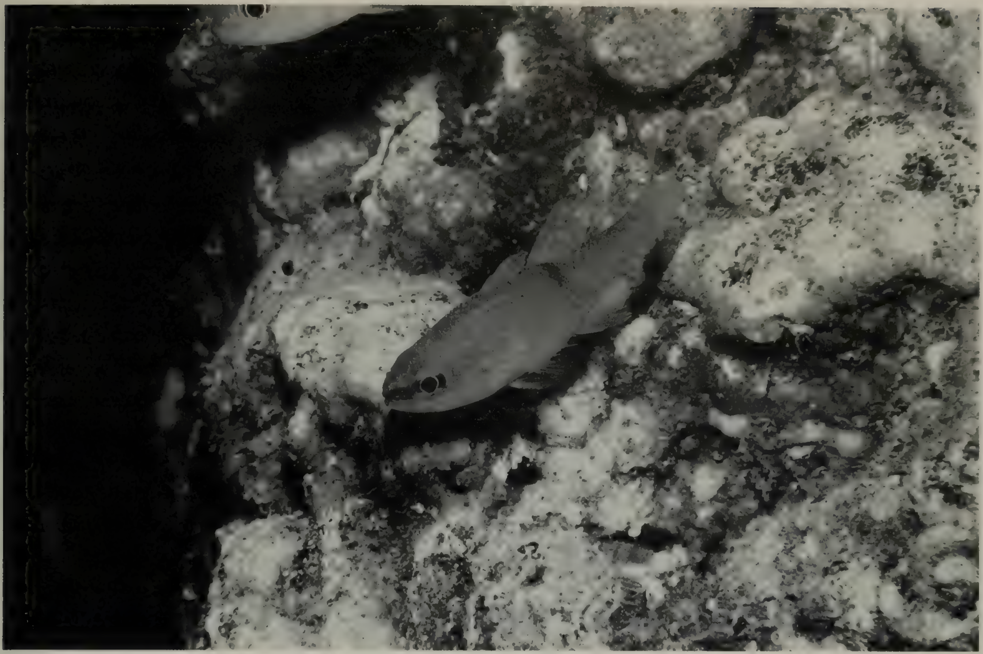


Fig. 2. Pink cardinalfish, *Apogon pacificus* at Bat Ray Cove San Clemente Island, 13 September 1998. Photo by Richard Herrmann.

The pink cardinalfish was accompanied by at least 15 Guadalupe cardinalfish, *A. guadalupensis,* in a small crevice at a depth of about 10 m. The smaller size and vertical bar set this fish off from the Guadalupe cardinalfish. The larger Guadalupe cardinalfish seemed to dominate the pink cardinalfish forcing it to the outer opening of the crevice. An individual pink cardinalfish was observed at North Coronado Island, Baja California, Mexico, 11 November 1998 (E. Hessel, pers. comm.). On 25 May 1998, Robert Snodgrass and Hugh Khim observed several pink cardinalfish in La Jolla Canyon, and in May 1998, several were collected by McConnaughey and Zerokski from the same location (Lea and Rosenblatt 2000).

Family Scaridae

Nicholsina denticulata (Evermann and Radcliffe 1917), loosetooth parrotfish

Previous reported range: Bahia Magdalena to Peru including the Gulf of California and the Galapagos Islands (Thomson et al. 1987).

Remarks.—Erik Erickson photographed both male and female loosetooth parrotfish, *Nicholsina denticulata,* off Pebbly Beach and Casino Point, Santa Catalina Island in May 1999 (Lea et al. 2001). This species was observed at the San Benito Islands, Baja California, Mexico in August 1998 (R. N. Lea and D. Richards, pers obs.) and photographed at Guadalupe Island, Baja California, Mexico in July 2000. Loosetooth parrotfish are well adapted to kelp beds. The coloration and shape allow it to be very cryptic, especially among *Eisenia arborea* blades.

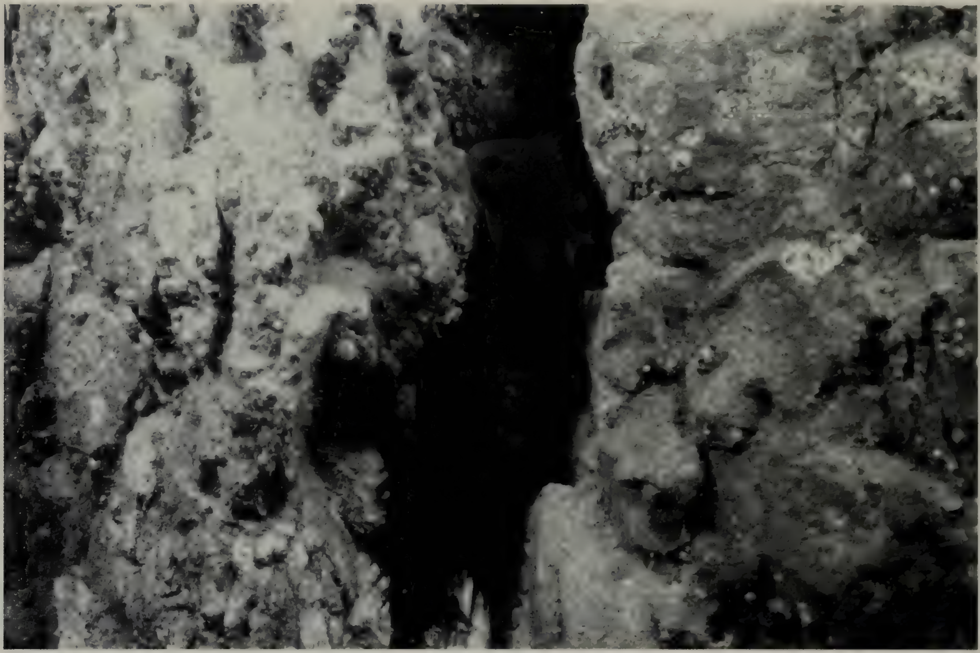


Fig. 3. Silverstripe chromis, *Chromis alta* at Casino Point, Santa Catalina Island, November 1998. Photo by Lorraine Sadler.

Family Pomacentridae

Chromis alta Greenfield and Woods 1980, silverstripe chromis

Previous reported range.—Thetis Bank, Mexico to Gulf of California and the Galapagos Islands (Greenfield and Woods 1980).

Remarks.—In November 1998, Erik Erickson and Lorraine Sadler observed and photographed an immature damselfish, around Casino Point Dive Park, Santa Catalina Island at a depth of 12–14 m. An additional sighting was made at a depth of 22 m at the SUEJAC in the northeast corner of the underwater park of possibly a second individual. Both fish were approximately 8–10 cm long. The sightings were originally reported as Cortez damselfish, *Stegastes rectifraenum,* however subsequent analysis of photos (Fig. 3) show the fish possessing blue striping consistent with juveniles of *Chromis alta* and lacking the dorsal spot generally observed on *S. rectifraenum.* Silverstripe chromis are also known from Islas San Benito, (R. N. Lea, collections made 1985–1990) and Isla Guadalupe (D. Richards, photos August 2000).

Range Expansions-New Island Records

Family Scorpaenidae

Scorpaenodes xyris (Jordan and Gilbert 1882), rainbow scorpionfish

Previous reported range.—Southern California to Peru including the Gulf of California and the Galapagos Islands. (Strachen et al. 1968).

Remarks.—Rainbow scorpionfish, *Scorpaenodes xyris,* like Guadalupe cardinalfish, is a shy crevice-dwelling species not commonly found at the islands. New island records for rainbow scorpionfish were noted with one individual found at Landing Cove, Anacapa Island (34°00.70 N, 119°21.71 W) on 25 September 1998 and one individual found in the vicinity of Cave Canyon, Santa Barbara Island, (33°28.68 N, 119° 01.56 W) 9 August 2000. Both juvenile and adult rainbow scorpionfish were commonly found at various sites around San Clemente Island and at several locations on Santa Catalina Island in both 1997 and 1998. Rainbow scorpionfish were very common at San Clemente Island in August 2000 with well over 100 found on a single dive at Bat Ray Cove. Smaller numbers were seen in Northwest Harbor. First collected in California in 1966 from San Clemente Island and 1967 from Santa Catalina Island (Strachan et al. 1968), this species now seems to be well established and spreading farther north.

Family Apogonidae
Apogon guadalupensis (Osburn and Nichols 1916), Guadalupe cardinalfish

Previous reported range.—Guadalupe Island to San Clemente Island (Hobson 1972) Islas San Benito (R. N. Lea and D. Richards pers. obs., August 1995)

Remarks.—Guadalupe cardinalfish, *Apogon guadalupensis,* was first recorded in California in 1967 (Hobson 1969) from the southern end of San Clemente Island. Most of these cardinalfish were small individuals approximately 50 mm in length. In 1971, an individual Guadalupe cardinalfish, about 100 mm long, was found during a night dive (Hobson 1972). Until 1997, sightings were remarkable. Throughout 1997 and especially 1998; *A. guadalupensis* were commonly found at various sites around San Clemente Island. We recorded Guadalupe cardinalfish as rare when we first found them at Seal Cove on the northwest side of San Clemente Island in June 1997. A year later we found 30 to 40 Guadalupe cardinalfish in Seal Cove. In 1998, we were finding more than 100 individuals on dives in Pyramid Cove, Smugglers Cove, and Bat Ray Cove where the small groups were spilling out of the rock cracks into open but protected spaces usually under an overhang. These fish were approximately 100–120 mm long. Hundreds were observed at Bat Ray Cove, down to a depth of at least 16 m. Male cardinalfish brood the eggs in their mouths during incubation and many brooding individuals were observed. Divers considered Guadalupe cardinalfish common and brooding males were observed at Bat Ray Cove in August 2000.

At least 20 Guadalupe cardinalfish were found in crevices along the eastern coast of Santa Barbara Island near Cave Canyon on 16 October 1997. Individuals were approximately 60–80 mm. This was the first record for Guadalupe cardinalfish at Santa Barbara Island. In 1998, Guadalupe cardinalfish were again found near Cave Canyon, Santa Barbara Island. Individuals were noticeably larger than in 1997, approximately 100 mm, and were apparently brooding eggs. No cardinalfish were found during a brief survey in 1999. Juvenile rockfish were often occupying the crevices where cardinalfish had been seen the year before. One individual, approximately 100 mm long, was found in the same vicinity during a dive on 9 August 2000. Another new island record occurred when two Guadalupe cardinalfish were found in Anacapa Landing Cove in July and again in August and September 1998 (D. Kushner et al. 1999).

Family Chaetodontidae

Chaetodon falcifer Hubbs and Rechnitzer 1958, scythe butterflyfish

Previous reported range.—Southern California (Santa Catalina Island) to Cabo San Lucus and the Galapagos Islands (Thomson et al. 1987).

Remarks.—Scythe butterflyfish, *Chaetodon falcifer,* have been known from Santa Catalina Island since 1965 (Freihofer 1966) and from La Jolla since 1970 (Kiwala and McConnaughey 1971). One individual was observed and photographed at San Pedro Point, on the east end of Santa Cruz Island on 13 August 1997 during a CIRP cruise. This fish was occupying a small cave at a depth of 7.5 m. A scythe butterflyfish, possibly the same individual, had been seen nearby several months earlier in deeper water (G. Gross, California Dept. of Fish and Game, pers. comm.). We have been unable to relocate the fish on repeated visits to the area.

Family Pomacentridae

Azurina hirundo Jordan and McGregor [in Jordan and Evermann 1898], swallow damselfish

Previous reported range.—Islas Revillagigedo to Santa Catalina Island (Lea and McAlary 1994).

Remarks.—Swallow damselfish, *Azurina hirundo,* sightings, while previously reported from the southern Channel Islands (Lea and McAlary 1994), are very rare. Two to four individual swallow damselfish were observed and photographed by Kathy deWet-Oleson in the summer of 1998 at Landing Cove, Anacapa Island. This is the first record of the species at Anacapa Island. A number of sightings were made in 1998 at the West End and Casino Point (E. Erickson, L. Sadler pers. comm.) on Santa Catalina Island. We observed a single swallow damselfish off Dune Point and 10–20 individuals at a depth of 10–13 m in Bat Ray Cove, San Clemente Island in September 1998. Two swallow damselfish were present at Bat Ray Cove on 13 August 2000. This species was also present at North Coronado Island on 5 June 1998 (R. Herrmann pers. comm.) and 11 November 1998. Typically these swallow damselfish were observed swimming with schools of blacksmith, *Chromis punctipinnis.*

Family Chaenopsidae

Chaenopsis alepidota (Gilbert 1890), orangethroat pikeblenny

Previous reported range.—Gulf of California (Thomson et al. 1987), Anacapa Island to Banderas Bay, Mexico (Stephans et al 1989).

Remarks.—Orangethroat pikeblenny, *Chaenopsis alepidota,* is well known from San Clemente and Santa Catalina Islands with a single population at King Harbor, Redondo Beach (Stephans et al. 1989). Orangethroat pikeblennies have been observed at Anacapa Island in low numbers since the 1983 El Niño (J. Engle, pers. obs.). In 1997, we observed them for the first time at Scorpion Anchorage, Santa Cruz Island (34°02.77 N, 119°32.81 W). Orangethroat pikeblennies were observed at Pelican Bay, Santa Cruz Island (34° 01.67 N, 119°42.24 W) on 12 May 1999 (D. Kushner, pers. comm.) and a juvenile was observed at Willow Cove, Santa Cruz Island in 1998 (J. Engle, pers. obs.) Courting males were common at Anacapa Island in August 1998, displaying above the *Chaetopterous variopedatus* worm tubes that they inhabited.

Family Diodontidae
Chilomycterus reticulatus Linnaeus 1758, spotfin burrfish

Previous reported range.—Southern California to the Galapagos Islands, Hawaii and Japan (Lea 1998).

Remarks.—Spotfin burrfish, *Chilomycterus reticulatus,* is another visitor recorded during previous El Niño events. First recorded in California in 1891 near San Pedro, specimens were collected in 1959 and 1982 (Lea and Vojkovich 1985), and observed in 1997 (SCMI 2000) off the southern California Mainland. One specimen of spotfin burrfish was found 3 September 1992, by CINP divers during a previous El Niño. The fish was captured by hand over a sand bottom in a depth of approximately 12 m off Arch Point, Santa Barbara Island (33°28.65 N, 119°01.73 W). This fish was photographed and measured (230 mm total length) before being released at the same location.

Other Observations—Increased Sightings

A number of southern fish species have been occasionally recorded at the Channel Islands or along the southern California mainland. The frequency of occurrence for several fish increased following the 1997–1998 El Niño.

Two juvenile California morays, *Gymnothorax mordax* (Ayres 1859), approximately 30–45 cm, were observed at Santa Catalina Island near Pumpernickel Cove during a CIRP cruise on 9 October 1999. California morays are rare to locally common in the Channel Islands and range from Magdalena Bay, Baja Calif. Mexico, to Pt. Conception (Miller and Lea 1972). Juveniles are rarely seen, however.

Juvenile California lizardfish, *Synodus lucioceps,* (Ayres 1855), were observed as abundant at sites along northeast Santa Cruz Island in August 1998. Ranging as far north as Puget Sound (Gonyea 1985), these fish are generally uncommon at the Channel Islands. We rarely see these fish except at deeper depths on silty bottoms and have never seen juveniles before. In 1998, we observed hundreds of juveniles (100–150 mm) over shallow (5–15 m) soft bottoms, some apparently feeding on mysids.

Purple brotula, *Oligopus diagrammus* (Heller and Snodgrass 1903), was first recorded in California, at San Clemente Island in 1966 (Strachan et al. 1968). During June 1997, and June and September 1998 cruises to San Clemente Island, purple brotula were found on several dives, mostly around Pyramid Head. Cabrillo Marine Aquarium divers (SCMI 2000) also reported it from Santa Catalina Island.

Mexican scad, *Decapterus scombrinus* (Valenciennes 1846), were observed at Bat Ray Cove, San Clemente Island (13 August 2000), Ship Rock, Santa Catalina Island (8 October and 18 November 1999), and Prince Island, San Miguel Island (15 November 1998) Islands. While ranging to at least central California occasionally (Miller and Lea 1972), these fish are uncommon in California. A yellowish belly, a finlet, and less pronounced lateral line arch distinguish Mexican scad from jack mackerel, *Trachurus symmetricus.*

Young-of-the-year garibaldi, *Hypsypops rubicundus* (Girard 1854), were observed at Santa Rosa Island in 1998 during a CINP cruise. Adult garibaldi are uncommon around Santa Rosa and this is our first record of a juvenile there. Occurrences of juvenile California sheephead, *Semiscossyphus pulcher* (Ayres

Table 1. Previous and new (1997–1998) records of tropical fishes at the California Channel Islands. P = previous and N = new. (1997–1998 El Niño).

		San Clemente	Santa Catalina	Santa Barbara	Anacapa	Santa Cruz
Apogon pacificus	pink cardinalfish	N				
Chromis alta	silverstreak chromis		N			
Nicholsina denticulata	loosetooth parrotfish		N			
Apogon guadalupensis	Guadalupe cardinalfish	P	P	N	N	
Scorpaenodes xyris	rainbow scorpionfish	P	P	N	N	
Azurina hirundo	swallow damselfish	P	P		N	
Chaetodon falcifer	scythe butterflyfish	P	P			N
Chaenopsis alepidota	orangethroated pikeblenny	P	P		P	N

1854), and rock wrasse, *Halichoeres semicinctus* (Ayres, 1859) were common at all islands. Juveniles of both species are rare to uncommon most years. California sheephead are known to recruit during El Niños (Cowan 1985).

Finescale triggerfish, *Balistes polylepis* Steindachner 1876, range from Chile to Pt. St. George, Del Norte Co. (Miller and Lea 1972), though are generally uncommon in southern California. Finescale triggerfish are reported from time to time at the islands and adults were observed on numerous occasions at Anacapa Island (Kathy deWet-Oleson, pers. comm.) during 1997–1998, mostly along the north side of West Anacapa Island. Finescale triggerfish were observed at North Coronado Island on 11 November 1998.

Discussion

During El Niño events, there is a lessening of the equatorward-flowing California Current and thus an increase in the northward transport (Hickey 1993). This change in current pattern of the Southern California Bight and the warm waters of El Niño provide the means for southern species to find their way to the Channel Islands. Some species may find refugia at the islands where they are able to persist.

Three tropical reef fishes (*Apogon pacificus, Nicholsina denticulata,* and *Chromis alta*), new to California in 1998, were observed at the Channel Islands. Five species previously recorded at one or more of the southern Channel Islands were documented at more northerly islands since 1997 (Table 1). An additional species, *Chilomycterus reticulatus,* was documented for the first time at the Channel Islands in 1992.

Santa Catalina Island typically has the warmest temperature regime for the Channel Islands (Engle and Richards 2001). As such we might expect the most tropical species records to occur there and indeed they do. The popularity of Santa Catalina Island dive sites and the fact that they are readily accessible by the resident divers on the island also lend the island to a greater number of sightings compared to other islands.

The south end of San Clemente Island consistently has been a good area for tropical fish. Large numbers of Guadalupe cardinalfish and rainbow scorpionfish along with the only sighting of pink cardinalfish and a moderate number of swallow damselfish were found in Bat Ray Cove just north of Pyramid Head. A number of tropical invertebrate species were observed in this same cove (Engle and Richards 2001) as were a number of warm-water algae including *Sporochnus pedunculatus, Spyridia filamentosa, Cutlaria cylindrica, Chondria californica,* and *Liagora californica.*

The numbers of juvenile rainbow scorpionfish and the brooding males of Guadalupe cardinalfish seem to indicate that some of these species have become well established. La Niña conditions may set back populations temporarily, as we saw with the decline of Guadalupe cardinalfish at Santa Barbara Island in 1999, but individuals can survive. Individuals of both Guadalupe cardinalfish and rainbow scorpionfish were observed in August 2000 at Santa Barbara Island. The first California records of Guadalupe cardinalfish were observed in the late 1960s at San Clemente Island and there was a subsequent decline by the early 1970s. In 1998, we were noting Guadalupe cardinalfish at San Clemente Island as common (10–100 individuals per dive) on fish counts, and though slightly less numerous, were still common during August 2000.

Recruitment for some species appears to be limited at the northern islands. The numbers of young-of-the-year sheephead, rock wrasse, and garibaldi observed in 1998 would seem to indicate increased recruitment during El Niño events. The increased recruitment may affect a species' ability to sustain itself on the margins of its range.

Shifts in the ichthyofauna associated with El Niño and La Niña have been documented before (see Cross and Allen 1993). The number of new species documented in southern California in this decade seems somewhat unprecedented however (various authors, this volume). The abnormally warm water throughout the period from 1992 through 1998 may have established conditions for more than just the occasional individual to expand its range and perhaps allowed the establishment of new colony populations.

Acknowledgments

Many individuals participated in the surveys that provided new records for subtropical fishes at the Channel Islands We thank the Channel Islands Research Program and the Channel Islands National Park research vessel crews and divers for their assistance, especially David Kushner for directing the CINP Kelp Forest Monitoring Program surveys. We thank Erik Erickson, Lorraine Sadler, Eric Hessell, George Gross and Kathy deWet-Oleson, Ventura, CA for providing additional records. Robert Lea, provided valuable taxonomic and biogeographic information. The Tatman Foundation (CIRP) and the National Park Service (CINP) sponsored the surveys. Additional observations were made during a research cruise sponsored by the U. S. Geological Survey, Biological Resources Division and the Love Lab (UCSB).

Literature Cited

Ayres, W. O. 1854. [Description of new fishes from California.] (Minutes of Academy meetings were printed in "The Pacific" (a newspaper) shortly after each meeting. New species accounts date to publication in The Pacific. Dates of publication are given in each species account). The Pacific (PACIFIC), v. 3 and 4 (thru no. 6).

Ayres, W. O. 1855. [Description of new species of California fishes.] A number of short notices read before the Society at several meetings in 1855. Proc. Calif. Acad. Sci. (Ser.1), v. 1 (pt 1): 23–77.

Ayres, W. O. 1859. [On new fishes of the Californian coast]. Proc. Calif. Acad. Sci. (Ser.1) v. 2 (1858–1862): 25–32.

Cowan, R. J. 1985. Large Scale patterns of recruitment by the labrid *Semicossyphus pulcher*, causes and implications. J. Mar. res. 43(3):719–742.

Cross, J.N. and L.G. Allen. 1993. Fishes. Pp. 459–540 *in* Ecology of the Southern California Bight (M.D. Dailey, D.J. Reish, and J.W. Anderson, eds.) University of California Press, xvi + 926 pp.

Davis, G.E., D.J. Kushner, J.M. Mondragon, J.E. Morgan, D. Lerma, and D. Richards. 1999. Kelp Forest Monitoring Handbook, Volume 1: Sampling Protocol. Channel Islands National Park. Ventura, California. 55 pp.

Engle, J. M. 1993. Distributional patterns of rocky subtidal fishes around the California Islands. Pp. 475–484 *in* Third California Islands Symposium: recent advances in research on the California Islands (F. G. Hochberg, ed.), Santa Barbara Museum of Natural History, xiii + 661 pp.

Engle, J. M. and D. V. Richards. 2001. New and unusual marine invertebrates discovered at the California Channel Islands during the 1997–1998 El Niño. Bull. So. Cal. Acad. Sci. 100: 186–198.

Evermann, B. W. and L. Radcliffe. 1917. The fishes of the west coast of Peru and the Titicaca Basin. Bull. U. S. Nat. Mus., 95:1–166.

Freihofer, W. C. 1966. New distributional records of the butterflyfish *Chaetodon falcifer*. Stanford Ich. Bull. 8(3): 207.

Gilbert, C. H. 1890. A preliminary report on the fishes collected by the steamer Albatross on the Pacific coast of North America during the year 1889, with descriptions of twelve new genera and ninety-two new species. Proc. U. S. Natl. Mus., 1 July, v. 13 (no.797):49–126.

Girard, C. F. 1854. Observations upon a collection of fishes made on the Pacific coast of the United States, by Lieut. W. P. Trowbridge, U. S. A., for the museum of the Smithsonian Institution. Proc. Acad. Nat. Sci. Phila. 7(no 4): 142–156.

Greenfield, David W. and Loren P. Woods. 1980. Review of the deep-bodied species of *Chromis* (Pisces: Pomacentridae) from the Eastern Pacific, with descriptions of three new species. Copeia (4): 626–641.

Gonyea, G. P. 1985. Occurrence of a juvenile California lizardfish, *Synodus lucioceps*, in Washington waters. Calif. Fish and Game 71(3):188.

Heller, E. and R. E. Snodgrass. 1903. Papers from the Hopkins Stanford Galapagos expedition, 1898–1899. XV. New Fishes. Proc. Washington Acad. Sci., 5:189–229.

Herre, A. W. C. T. 1935. New fishes obtained by the Crane Pacific expedition. Field Mus. Nat. Hist. Publ. Zool. Ser., 15 Feb., v. 18(no. 12):383–438.

Hickey, B. M., 1993. Physical oceanography. Pp. 19–70 *in* Ecology of the Southern California Bight (M.D. Dailey, D.J. Reish, and J.W. Anderson, eds.) University of California Press, xvi + 926 pp.

Hobson, E.S. 1969. First California record of the Guadalupe cardinalfish, *Apogon guadalupensis* (Osburn and Nichols), Calif. Fish and Game, 55(2):149–151.

Hobson, E.S. 1972. The survival of Guadalupe cardinalfish Apogon guadalupensis at San Clemente Island. Calif. Fish and Game 58(1): 68–69.

Hubbs, C. L. and A. B. Rechnitzer. 1958. A new fish, *Chaetodon falcifer* from Guadalupe Island, Baja California, with notes on related species. Proc. California Acad. Sci., Ser. 4 29(8): 272–313.

Jordan, D. S. and B. W. Evermann. 1898. The fishes of North and middle America. U. S. Natl. Mus. Bull. (47): 1241–2183.

Jordan, D. S. and C. H. Gilbert. 1882. Catalogue of the fishes collected by Mr. John Xantus at Cape San Lucas, which now are in the United States National Museum, with descriptions of eight new species. Proc. U. S. Natl. Mus., 16 Sept., v. 5(no. 290): 353–371.

Kiwala, R. S. and R. R. McConnaughey. 1971. A second record of the scythe butterflyfish, *Chetodon falcifer*, from California. California Fish and Game, 57(3): 217–218.

Kushner, D. J., D. Lerma, S. Alesandrini, and J. Shaffer. 1999. Kelp Forest Monitoring 1998 Annual Report. Channel Islands National Park, Ventura California. 68 pp.

Lea, R. N. 1998. The spotfin burrfish—an infrequent visitor. Tidelines 18(1):8.

Lea, R. N., E. D. Erikson, K. Boyle and R. Given. 2001. Occurrence of the loosetooth parrotfish, *Nicholsina denticulata* (Scaridae), from Santa Catalina Island, California. Bull. So. Cal. Acad. Sci. 100: 167–169.

Lea, R. N. and F. McAlary. 1994. Occurrence of the swallow damselfish, *Azurina hirundo,* from islands off southern California. Bull. So. Cal. Acad. Sci., 93(1):42–44.

Lea, R. N. and R. H. Rosenblatt. 1992. The Cortez grunt (*Haemulon flaviguttatum*) recorded from two embayments in southern California. Calif. Fish and Game. 78(4):163–165.

Lea, R. N. and R. H. Rosenblatt. 2000. Observations on fishes associated with the 1997–98 El Niño off California. CalCOFI Reports, Vol. 41:117–129.

Lea, R. N. and M. Vojkovich. 1985. Record of the Pacific Burrfish from Southern California. Bull. Southern California Acad. Sci. 84(1): 46–47.

Linnaeus, C. 1758. Systema Naturae, Ed. X. (Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, Locis. Tomusl. Editio decima, reformata.) Holmaiae. Systema Nat. ed. 10, 1 Jan., v.1: i-ii+1–824.

McPhaden, M. J. 1999. Genesis and Evolution of the 1997–98 El Niño. Science: 283:950–954.

Miller, D. J. and R. N. Lea. 1972. Guide to the Coastal Marine Fishes of California. Department of Fish and Game, Fish Bulletin, No. 157, 235 pp.

Osburn, R. C. and J. T. Nichols. 1916. Shore fishes collected by the "Albatross" expeditions in Lower California with descriptions of new species. Bull. Amer. Mus. Nat. Hist., 35(16):139–181.

Radovitch, J. 1961. Relationships of some marine organisms of the northeast Pacific to water temperatures. Calif. Dept. Fish and Game, Fish Bull. No. 112, 62 pp.

SCMI. 2000. Southern California Marine Institute, Unusual Fish Sightings internet web site. *http://www-bcf.usc.edu/~scmi/xfishpg.html.*

Steindachner, F. 1876. Ichthyologische Beiträge (V)[Subtitles 1-v.]. Sitzungsber. Akad. Wiss. Wien, v. 74(1.Abth.): 49–240.

Stephans, J. S. Jr., M. Singer, and L. Targgart. 1989. Notes on the first record of orangethroat pickblenny, *Chaenopsis alepidota* (Gilbert), in mainland California. California Fish and Game 75: 180–183.

Strachan, Alec R., Charles H. Turner, and Charles T. Mitchell. 1968. Two fishes and a mollusk, new to California's marine fauna, with recent comments regarding other recent anomalous occurrences. California Fish and Game, 54(1): 49–57.

Thomson, D. A., L. T. Findley, A. N. Kerstitch. 1987. Reef Fishes of the Sea of Cortez. University of Arizona Press, xviii + 302 pp.

Valenciennes, A. 1846. Table + Ichthyology Pls. 1–10. In: A. du Petit-Thouars. Atlas de Zoologie. Voyage autour du monde sur la frégate "Vénus", pendant les années 1836–1839. Voyage Venus.

Accepted for publication 22 December 2000.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 186–198

New and Unusual Marine Invertebrates Discovered at the California Channel Islands during the 1997–1998 El Niño

John M. Engle[1] and Daniel V. Richards[2]

[1]*Tatman Foundation and Marine Science Institute, University of California, Santa Barbara, California 93106 Phone: 805-893-8547 Fax: 805-893-8062*
Email: j_engle@lifesci.ucsb.edu
[2]*Channel Islands National Park, 1901 Spinnaker Drive, Ventura, California 93001*

Abstract.—The occurrence of new and unusual subtropical invertebrates at the Channel Islands was documented for the exceptional 1997–1998 El Niño and subsequent 1998–2000 La Niña during periodic shallow subtidal surveys. Six species (*Chloeia viridis, Stenorhynchus debilis, Pleurobranchus areolatus, Chromodoris galexorum, Polycera alabe,* and *Holothuria impatiens*) were new to California. Six others (*Bunodeopsis* sp., *Hemisquilla ensigera californiensis, Dromidia larraburei, Pteria sterna, Arbacia incisa,* and *Centrostephanus coronatus*) represented new records at one or more islands. Most new records occurred at the southernmost and easternmost islands (Santa Catalina, San Clemente, and Anacapa). Repeated sightings of progressively larger size classes provided recruitment, growth, and survivorship information for five species. Increased sightings of subtropical species in California likely are due to northward shifts of biogeographic provinces that occurred during more than two decades of above average seawater temperatures.

The California Channel Islands support a great diversity of nearshore marine life, due primarily to their location within the Southern California Bight, astride the transition between warm subtropical waters of the Californian Province to the south and cold temperate waters of the Oregonian Province to the north. The complex mixing of warm and cold water masses results in unique oceanographic conditions influencing each of the eight islands (Fig. 1), which in turn affect the distribution of plant, invertebrate, fish, bird, and mammal species. Overall, there is an obvious southeast (i.e., Santa Catalina Island) to northwest (i.e., San Miguel Island) trend of decreasing sea surface temperatures among the islands that correlates well with differences in the composition of species assemblages (Engle 1993, 1994). Individual species distributions may shift northwesterly or southeasterly over time at the islands, depending on the magnitude and duration of warm-water (e.g., El Niño) or cold-water (e.g., La Niña) regimes. New sightings of subtropical species typically are associated with major El Niño events (e.g., Radovich 1961; Strachan et al. 1968).

Southern California waters have experienced a long-term warming trend that began in 1976, including major El Niño events in 1983–1984, 1986–1987, 1992–1993, and 1997–1998. Of these, the 1983–1984 and 1997–1998 El Niños were two of the strongest on record with some of the highest temperature anomalies ever recorded (McPhaden 1999). During the recent El Niño, the Southern California

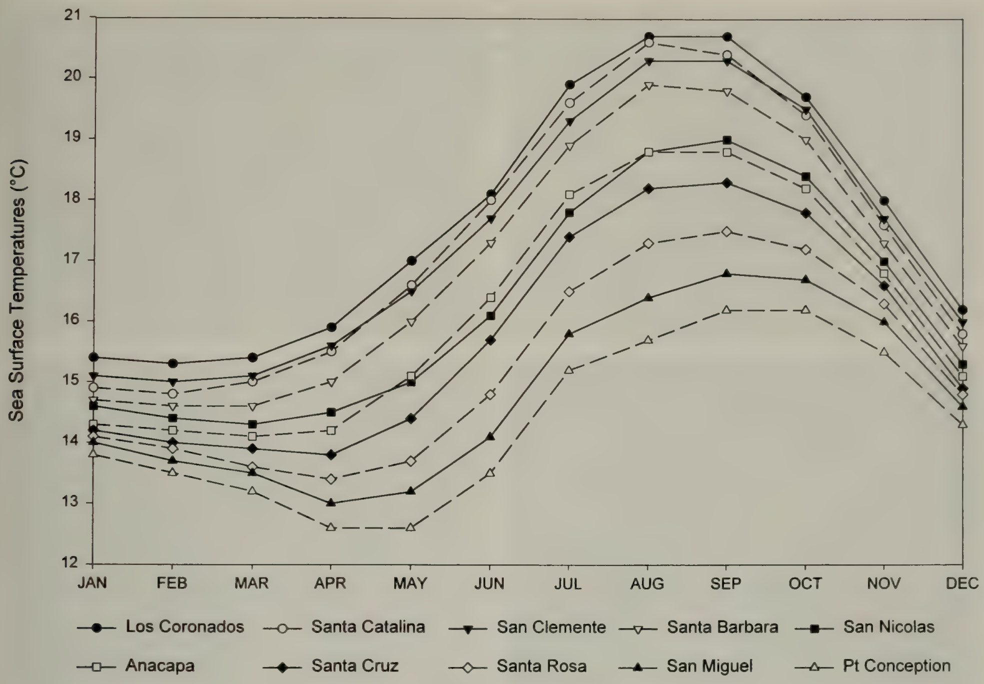


Fig. 1. Mean monthly sea surface temperatures at the eight Channel Islands for the period 1982–1999. Data were taken from National Weather Service (Monterey) oceanographic analyses.

Bight experienced above normal sea temperatures for 1.5 yr, from May 1997 to August 1998 (CoastWatch Bulletins 1997–2000). By September 1998, the El Niño abruptly switched to La Niña, which caused cooler temperatures also for ~1.5 yr, from September 1998 to March 2000 (CoastWatch Bulletins 1997–2000).

This paper presents new distributional records for shallow-water subtropical invertebrates at the California Channel Islands during and after the 1997–1998 El Niño. New and unusual fish records at the Channel Islands are reported in a companion paper by Richards and Engle (this volume). Post-El Niño records are important because some species that recruit during the warm-water period are slow-growing and only become evident after attaining larger sizes. Periodic surveys allow determination of growth and survivorship of these exotic species. The invertebrate observations we report here include six subtropical species seen for the first time in California waters as well as six other species that have newly appeared (or have notably increased abundances) at one or more of the eight Channel Islands (Table 1). We have noted some southern California mainland sightings, but have not attempted to include all new mainland records for these species.

Methods

The eight Channel Islands off the southern California coast have been surveyed periodically since 1980 in cooperative studies by the Tatman Foundation's Channel Islands Research Program (CIRP) and Channel Islands National Park (CINP) Kelp Forest Monitoring Program. CINP divers regularly survey 16 fixed sites at five islands to monitor population dynamics of key algal, invertebrate, and fish

Table 1. Previous and new (1997–1998 El Niño) records for 12 species of subtropical marine invertebrates at the eight California Channel Islands. Abbreviations: Islands: SCL = San Clemente, SCA = Santa Catalina, SBA = Santa Barbara, SNI = San Nicolas, ANA = Anacapa, SCR = Santa Cruz, SRO = Santa Rosa, and SMI = San Miguel; Records: P = previous and N = new (1997–1998 El Niño).

		California Channel Island							
Phylum	Species	SCA	SCL	SBA	SNI	ANA	SCR	SRO	SMI
Cnidaria	*Bunodeopsis* sp.	N	N						
Annelida	*Chloeia viridis*	N							
Arthropoda	*Dromidia larraburei*					N			
	Hemisqulla ensigera	P	P			P	P		
	Stenorhynchus debilis	N	N			N			
Mollusca	*Chromodoris galexorum*	N							
	Pleurobranchus areolatus	N	N			N			
	Polycera alabe	N		N		N			
	Pteria sterna	P	P	P		N	N	N	
Echinodermata	*Arbacia incisa*	N	N	N		N	N		
	Centrostephanus coronatus	P	P	P	P	P	P	N	
	Holothuria impatiens	N							

species. Invertebrates are quantified using random point contact, quadrat, and transect techniques (Davis et al. 1999). CIRP divers conduct qualitative reconnaissance surveys at a broader spectrum of locations at all eight islands to provide an overview of island marine assemblages. Both programs include general search methods to note unusual species at each survey site. Voucher collections and photographs or videographs maintained at CIRP and California museums (primarily the Natural History Museum of Los Angeles County (NHMLAC)) are utilized to additionally document new sightings whenever possible. Latitude/longitude coordinates are provided for island sites not named on National Oceanic and Atmospheric Administration nautical charts.

First Occurrences in California

Phylum Annelida Class Polychaeta Order Amphinomida Family Amphinomidae *Chloeia viridis* Schmarda 1861 Ornate fireworm (Fig. 2A)

Previous reported range.—Throughout the Gulf of California to Panama, and the entire Caribbean; intertidal and subtidal to at least 91 m (Hartman 1940; Brusca 1980; Kerstich 1989).

First Channel Islands records.—Over 70 fireworms observed on stable sand habitats at Santa Catalina Island during October 1998 to May 2000. Sites: Willow Cove (>60 specimens) at 9–21 m depths (10/98, 5/99, 6/99, 10/99); Empire Landing (>10 specimens) at 12–20 m depths (5/00). Vouchers: photographs (E. Erikson) and specimens (NHMLAC).

Remarks.—*Chloeia viridis* is a distinctive polychaete with long venomous setae. Though common throughout the Gulf of California (Brusca 1980), there are no records from the Pacific Coast of Baja California (L. Harris, pers. comm.). One of us (Engle) has surveyed mantis shrimp (*Hemisquilla ensigera californiensis*) at least annually since 1984 at Willow Cove, yet *Chloeia* was not found

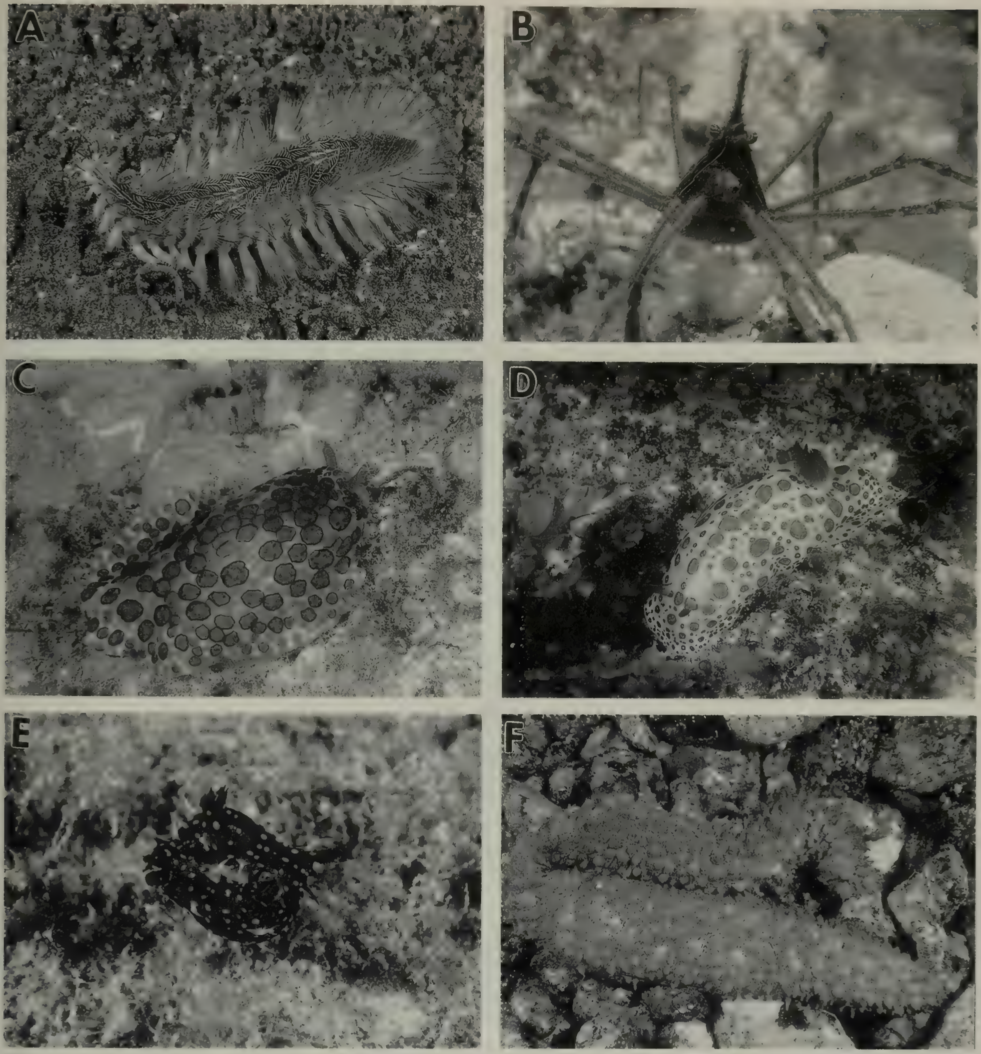


Fig. 2. Warm-water invertebrates representing first occurrences in California. A. *Chloeia viridis*. B. *Stenorhynchus debilis*. C. *Pleurobranchus areolatus*. D. *Chromodoris galexorum*. E. *Polycera alabe*. F. *Holothuria impatiens*. Photos A, C–F by E. Erikson. Photo B by R. Herrmann.

prior to 10/98. No specimens have been reported elsewhere in California. *C. viridis* was observed crawling on the surface of sheltered-shore, silty-sand substrates and entering tubes of the parchment worm *Chaetopterus variopedatus*. On several occasions, fireworms appeared to be feeding on bat ray (*Myliobatis californica*) feces, and in two instances, an individual was seen consuming the sea slug *Navanax inermis*.

Phylum Arthropoda Class Malacostraca Order Decapoda Family Majidae
Stenorhynchus debilis (Smith 1871) Panamic arrow crab (Fig. 2B)

Previous reported range.—Guadalupe Island (Baja California) (M. Wicksten pers. comm.) and Gulf of California to Chile and the Galapagos Islands; intertidal and subtidal to 61 m (Brusca 1980; Kerstich 1989; Gotshall 1998).

First Channel Islands records.—Several hundred arrow crabs observed at 3–23 m depths on rocky substrata at three islands during March to October 1998. Santa Catalina Island: Pebbly Beach, Casino Point, and Ripper's Cove (>100 specimens, E. Erikson, 3/98); Bird Rock, Lion's Head, and Blue Cavern Point (L. Roberson, 3-7/98); and West End (9 specimens, 10/98). San Clemente Island: Mosquito Cove (1 specimen, 5/98); E. Pyramid Cove (2 specimens, 5/98); Pyramid Head (>100 specimens, 5/98, 9/98); Purse Seine Rock (1 specimen, 5/98); and Seal Cove (1 specimen, 9/98). Anacapa Island: Frenchy's Cove (1 specimen, 8/98). Vouchers: photographs (E. Erikson, R. Herrmann) and specimens (NHMLAC).

Remarks.—*Stenorhynchus debilis* was observed by various scuba divers at Santa Catalina and San Clemente Islands and along the southern California mainland from Mission Bay to Redondo Beach in spring/summer 1998 (C. Gramlich & D. Cadien pers. comm.). Also, it was collected in trawling surveys around Santa Catalina Island (7/98) and off Huntington Beach (8/99) (see Montagne & Cadien this volume). This short-lived crab is seasonal in the Gulf of California, attaining maximum sizes in May to July (Kerstich 1989). We observed peak abundances in spring (few small crabs; most moderated-sized) and summer 1998 (most large), with only a few heavily-fouled individuals seen in fall 1998 (all large), and none thereafter. Two spring-collected specimens survived in aquaria until fall 1998. *S. debilis* mostly occurred in small crevices or under the spine canopy of the coronado sea urchin *Centrostephanus coronatus* (29 of 667 *C. coronatus* surveyed had a sheltering arrow crab at Pyramid Head on 5/18/98). Some crabs were found under rocks or mooring blocks in sheltered silty coves (E. Erikson pers. comm.).

Phylum Mollusca Class Gastropoda Order Notaspidea Family Pleurobranchidae
Pleurobranchus areolatus Mörch 1863 Warty sea slug (Fig. 2C)

Previous reported range.—San Benitos and Cedros Islands (Baja California) (D. Behrens pers. comm.), Gulf of California to Ecuador, throughout the Caribbean and tropical west Africa; intertidal and subtidal to 31 m (Keen 1971; Kerstich 1989).

First Channel Islands records.—Seven individuals found at 5–22 m depths on rocky reefs at three islands during June 1998 to June 1999. Santa Catalina Island: Casino Point (1 specimen, E. Erikson, 6/98) and West End (1 specimen, 10/98). San Clemente Island: Pyramid Head (2 specimens, 9/98) and Purse Seine Rock (32° 52.48′ N, 118° 24.94′ W) (2 specimens, 6/99). Anacapa Island: Frenchy's Cove (1 specimen, 8/98). Vouchers: photographs (E. Erikson, R. Herrmann, D. Richards) and specimens (D. Behrens). Also, P. Haaker and M. Tegner (pers. comm.) collected two specimens at San Clemente Island in August 1998.

Remarks.—*Pleurobranchus areolatus* is a large (~10-15 cm) distinctive opisthobranch, whose dorsal surface is covered with warty orange and reddish-brown tubercles. Variations in color patterns and tubercle morphology among the specimens raise suspicions that some individuals represent an undescribed *Pleurobranchus* (D. Behrens, pers. comm.); however, these variations may be within the range of characters exhibited by *P. areolatus.* Several specimens were collected during the same period on the mainland at La Jolla (D. Behrens, pers. comm.).

Phylum Mollusca Class Gastropoda Order Nudibranchia Family Chromodorididae

Chromodoris galexorum (Bertsch 1978) Galactic sea slug (Fig. 2D)

Previous reported range.—Guadalupe and Cedros Islands (Baja California) to the Gulf of California; subtidal 3–45 m (Bertsch 1978; Bertsch and Kerstich 1984; Kerstich 1989).

First Channel Islands records.—Five galactic nudibranchs found on rocky reefs along north side of Santa Catalina Island at 10–18 m depths during October 1998 to May 2000. Sites: Ship Rock (1 specimen, 10/98); Blue Cavern Point (1 specimen, 5/00); and Long Point (3 specimens, E. Erikson, 5/00). Vouchers: photographs (E. Erikson, D. Richards) and specimens (D. Behrens).

Remarks.—*Chromodoris galexorum* is a colorful nudibranch, with red rhinophores and gills and yellow-ringed reddish spots on a creamy white background. The previous northern limit at Guadalupe Island was considered an anomaly due to El Niño conditions (Kerstich 1989). The live specimen from Big Fisherman Cove was 83 mm long, more than double the reported size range of 19–38 mm (Kerstich 1989).

Phylum Mollusca Class Gastropoda Order Nudibranchia Family Polyceratidae

Polycera alabe Collier & Farmer 1964 Inkstain nudibranch (Fig. 2E)

Previous reported range.—Cedros Island (Baja California) to the Gulf of California; intertidal and subtidal (Keen 1971; Behrens 1991; Kerstich 1989).

First Channel Islands records.—Three inkstain nudibranchs observed at 8–15 m depths on rocky reefs at three islands from June to September 1998. Santa Catalina Island: Italian Gardens (33° 24.64′ N, 118° 22.75′ W) (1 specimen, E. Erikson, 6/98). Santa Barbara Island: Arch Point (1 specimen; 9/98). Anacapa Island: Cathedral Cove (34° 00.71′ N, 119° 22.29′ W) (1 specimen; 8/98). Vouchers include photographs (E. Erikson) and video (D. Kushner).

Remarks.—*Polycera alabe* is a small, blue-black, orange-spotted nudibranch that feeds on bryozoans (Kerstich 1989).

Phylum Echinodermata Class Holothuroidea Order Aspidochirotida Family Holothuriidae

Holothuria impatiens (Forskål 1775) Brown spotted sea cucumber (Fig. 2F)

Previous reported range.—Rosario Bay (Baja California) and throughout the Gulf of California to Ecuador and the Galapagos Islands, circumtropical; intertidal and subtidal to 46 m. (Brusca 1980; Kerstich 1989; Hendler et al. 1995; Gotshall 1998).

First Channel Islands records.—Three individuals were found at 5–8 m depths under rocks at Pebbly Beach, Santa Catalina Island during November 1998 (E. Erikson, 1 juvenile and 1 adult 25 cm long) and May 2000 (1 adult ~21 cm long). Vouchers: photographs (E. Erikson) and specimens (NHMLAC).

Remarks.—*Holothuria impatiens* adults were golden-brown with numerous papillae. The juvenile was a lighter cream color. All individuals eviscerated when handled out of water.

New Records at One or More Channel Islands

Phylum Cnidaria Class Anthozoa Order Actiniaria Family Boloceroididae
Bunodeopsis sp. Stinging sea anemone

Previous reported range.—Mission Bay (San Diego) and Puerto Escondido (Baja California); shallow subtidal (J. Ljubenkov 1995).

New Channel Islands records.—Bunodeopsis were found as locally abundant epibionts on eelgrass (*Zostera marina*), surfgrass (*Phyllospadix* spp.), and various brown algae at 3–15 m depths on sheltered sand and rock habitats at two islands from May 1996 to August 2000. Santa Catalina Island: Big Fisherman Cove (hundreds on *Zostera,* 9/97); Catalina Harbor (few on *Zostera,* 4/98); and Isthmus Cove (L. Roberson, locally common on *Macrocystis pyrifera, Eisenia arborea, Cystoseira neglecta* and other brown algae, 9/98). San Clemente Island: Purse Seine Rock (hundreds on *Zostera,* 5/96, 9/98, 8/00) and Pyramid Head (abundant on *Phyllospadix, Sargassum palmeri, Zonaria farlowii,* and miscellaneous brown algae, 9/98). Vouchers: photographs (R. Herrmann, L. Roberson).

Remarks.—Bunodeopsis is a tiny translucent white sea anemone that was discovered on eelgrass in Mission Bay (San Diego) in 1995, where its extensive cover contributed to a decline in *Zostera* populations (Sewell & Williams 1995). This little-known representative of a subtropical/tropical genus is thought to be an undescribed species (Ljubenkov 1995). The anemone is capable of autotomizing tentacles, drifting with currents, and stinging exposed skin of divers (Ljubenkov 1995).

Phylum Arthropoda Class Malacostraca Order Stomatopoda Family Hemisquillidae
Hemisquilla ensigera californiensis (Stephenson 1967) Mantis shrimp

Previous reported range.—Point Conception (Santa Barbara County) to the Gulf of California and Panama; subtidal to 91m (Brusca 1980; Morris et al. 1980; Kerstich 1989; Gotshall 1994; Jensen 1995).

New Channel Islands records.—Hemisquilla have been present or common at 8–21 m depths in stable sand habitats at Santa Catalina and San Clemente Islands, but rare at Anacapa and Santa Cruz Islands (Basch and Engle 1993; J. Engle unpub. data.). During the 1997–1998 El Niño, recruitment was evident and abundances increased at surveyed island sites. Santa Catalina Island: Cherry Cove (common: 9/97, 4/98); Big Fisherman Cove (common: 9/97, 4/98); Willow Cove (adults common, juveniles abundant: 9/97, 10/98) (adults present, juveniles rare: 5/99, 6/99, 10/99); Big Geiger Cove (33° 27.58′ N, 118° 31.04′ W) (common: 4/98, 4/99); Catalina Harbor (common: 4/98); Parson's Landing (present: 4/98); East End (common: 9/98), Arrow Point (present: 4/99); and Empire Landing (present: 5/00). San Clemente Island: Purse Seine Rock (common: 5/98, 9/98, 8/00). Anacapa Island: Frenchy's Cove (present: 6/98, 8/98, 7/99, 6/00) and Cathedral Cove (present: 6/98). Santa Cruz Island: Scorpion Cove (present: 8/98, 8/99); Prisoner's Cove (present: 8/98); Potato Harbor (present: 8/99); Twin Harbor (present: 8/99); Smuggler's Cove (present: 6/00); and Hazard's Anchorage (present: 8/99). The sightings at Prisoner's Harbor, Twin Harbor, and Hazards Anchorage represent new northwestern island records.

Remarks.—Hemisquilla ensigera californiensis is a large but cryptic mantis shrimp that inhabits burrows in sheltered sand habitats. This species typically closes its burrow entrance with a plug of sand during bright midday hours (Basch and Engle 1989); therefore, abundances likely were underestimated except at Willow Cove where population dynamics have been monitored since 1984 (Engle unpub. data). Also *Hemisquilla* can occur at depths to 70 m (Basch and Engle 1993), but our surveys were limited to 21 m depths. Stomatopod burrow densities increased nearly ten-fold at Willow Cove during 1996–1998 (0.01/m^2 (1995), 0.1/m^2 (1996), 0.06/m^2 (1997), 0.1/m^2 (1998), 0.01/m^2 (1999)), with 80% of the increase due to additional small (<20 mm diameter) burrows.

Order Decapoda Family Dromiidae
Dromidia larraburei Rathbun 1910 Sponge crab

Previous reported range.—Monterey Bay and Long Beach to Magdalena Bay (Baja California), the Gulf of California, Peru and the Galapagos Islands; intertidal and subtidal to at least 18 m (Schmitt 1921; Brusca 1980; Kerstich 1989).

New Channel Islands records.—Three individuals were found on a stable sand slope at Frenchy's Cove, Anacapa Island in June 1998 (paired male and female) and July 1999 (1 female) in 6–7 m depths. Vouchers: photographs (J. Carroll, E. Erikson) and specimens (NHMLAC).

Remarks.—Dromidia larraburei is a small, cryptic anomuran crab known for using its modified fifth leg to hold a sponge on its back (Kerstich 1989); however, the 6/98 male and 7/99 female at Anacapa Island were holding brown bubble kelp (*Colpomenia sinuosa*) over their bodies. The freshly-molted 6/98 female held by the male was soft and pink. *Dromidia* settled in large numbers on Mission Bay Reef (San Diego) in spring 1998, were still abundant in early 1999, then disappeared by August 1999 (C. Gramlich pers. comm.).

Phylum Mollusca Class Bivalvia Order Pterioida Family Pteriidae
Pteria sterna (Gould 1851) Pacific wing-oyster

Previous reported range.—Venice (Los Angeles County) and Santa Barbara Island to Morro Santo Domingo (Baja California), throughout the Gulf of California to Peru and the Galapagos Islands; subtidal 1–25 m (Keen 1971; Brusca 1980; Coan et al. 2000).

New Channel Islands records.—Pteria commonly observed attached to gorgonians at 6–23 m depths at numerous sites around all Channel Islands except San Nicolas and San Miguel during the period September 1998 to August 2000. Santa Catalina Island: Church Rock (9/98); Salta Verde Point (9/98); Ship Rock (10/98, 4/99, 10/99, 5/00); West End (10/98); Willow Cove (on buoy lines: 10/98, 5/99, 10/99); Blue Cavern Point (4/99); Bird Rock (8/98 (L. Roberson), 4/99, 5/00); Arrow Point (4/99); Long Point (10/99, 5/00); Eagle Reef (5/00); and Hen Rock (5/00). San Clemente Island: Dune Point (33° 01.58′ N, 118° 33.80′ W) (9/98); Northwest Harbor (9/98); Pyramid Head (9/98, 8/00); and W Pyramid Cove (9/99, 8/00). Santa Barbara Island: Southeast Sea Lion (33° 27.45′ N, 119° 01.52′ W) (10/98, 7/99, 6/00); South End (9/99); Arch Point (9/99); Sutil Island (8/00); and Landing Cove (8/00). Anacapa Island: Landing Cove (34° 00.70′ N, 119° 21.71′ W) (10/98); Admiral's Reef (34° 00.33′ N, 119° 25.86′ W) (7/99); Cathedral Cove (7/99); Cat Rock (8/99); Survey Rock (34° 00.66′ N, 119° 22.28′ W)

(6/00); and West End (6/00). Santa Cruz Island: Potato Rock (8/99); Cavern Point (8/99); Twin Harbor (8/99); Hazards Anchorage (34° 03.61′ N, 119° 49.73′ W) (8/99); Forney Cove (8/99); Gull Island (8/99); Blue Banks Anchorage (8/99); and San Pedro Point (8/99). Santa Rosa Island: Johnson's Lee (7/99). Vouchers: photographs (E. Erikson, R. Herrmann, D. Richards) and specimens (J. Engle).

Remarks.—Pteria sterna have appeared in southern California during previous warm-water periods, but have not established permanent populations (Coan et al. 2000, Engle unpub. data). Prior distributional records for these "pearl" oysters at the Channel Islands have been sparse, and their association with sea fans (Order Gorgonacea) not well documented (Keen 1971, Brusca 1980, Coan et al. 2000). Except for several wing-oysters found attached to subsurface float lines at Willow Cove, all *Pteria* encountered were attached to shallow-water gorgonians, including *Muricea californica, M. fruticosa, Lophogorgia chilensis,* and *Eugorgia rubens.* Smaller individuals (5–9 cm) predominated in 1998 (shell length variability mainly was due to size differences in the anterior spike-like wing). Most *Pteria* were large in 1999 and 2000 (10–15 cm). Largest individuals exceeded the published size limits of 10 cm (Keen 1971, Brusca 1980, Coan et al. 2000). At Willow Cove, three *Pteria* on float lines grew on average from 6.5 to 12 cm in one year (10/98 to 10/99). Increased numbers of empty shells were observed at many sites in 2000.

Phylum Echinodermata Class Echinoidea Order Arbacioida Family Arbaciidae
Arbacia incisa (Agassiz 1863) Arbacia sea urchin

Previous reported range.—Newport Bay (Orange County) and Gulf of California to Peru, and the Galapagos Islands; intertidal and subtidal to 90m (H. L. Clark 1948; Brusca 1980; Morris et al. 1980; Gotshall 1998).

New Channel Islands records.—Several dozen *Arbacia* found in rocky crevices and artificial recruitment modules (ARM's) (Kushner et al. 1999) at 5–18 m depths at five islands during May 1998 to September 2000. Santa Catalina Island: Pebbly Beach (1 juvenile, E. Erikson, 10/98). San Clemente Island: Purse Seine Rock (1 juvenile, 5/98). Santa Barbara Island: Southeast Sea Lion (2 found in twenty-four 0.25 m^2 quadrats in 9/98; 6 in 6/99, 3 in 6/00). Anacapa Island: Admiral's Reef (ARM: 1 each in 8/98 (10 mm), 8/99, and 8/00 (35 mm)); Landing Cove (ARM: 1 juvenile in 8/98); and Cathedral Cove (ARM: 1 each in 7/98 (12 mm), 7/99, and 9/00 (32 mm)). Santa Cruz Island: Gull Island (ARM: 1 each in 7/98 (7 mm) and 9/99). Vouchers: photographs (E. Erikson) and specimens (NHMLAC).

Remarks.—Arbacia incisa was not previously known from the Channel Islands. Most individuals (8-10 mm diameter recruits in 1998 and larger individuals in 1999 and 2000) were found in concrete recruitment modules surveyed by Channel Islands National Park. Three juveniles raised in aquaria grew from 8-10 mm in spring 1998 to 27–33 mm in spring 2000 to 29–36 mm in fall 2000. *Arbacia* also were found in San Diego (C. Gramlich, Mission Bay in 4/97 and 1/99).

Order Diadematoida Family Diadematidae
Centrostephanus coronatus (Verrill 1867) Coronado sea urchin

Previous reported range.—California Channel Islands to the Gulf of California to Peru, and the Galapagos Islands; intertidal to 125m (Brusca 1980; Morris et al. 1980; Gotshall 1994; Kerstich 1989).

New Channel Islands records.—In prior years, *Centrostephanus coronatus* has been common/abundant at San Clemente and Santa Catalina Islands, uncommon/rare at Santa Barbara, San Nicolas, Anacapa, and Santa Cruz Islands, and absent at Santa Rosa and San Miguel Islands (J. Engle, unpub. data). Large-scale recruitment of 5–25 mm (test diameter) *Centrostephanus* was documented during surveys and in ARM's (Kushner et al. 1999) at numerous island sites during spring to fall 1998 (and in some ARM's in summer 1999). Santa Catalina Island: Indian Rock (4/98); Blue Cavern Point (4/98); Bird Rock (4/98); Church Rock (9/98); Ship Rock (10/98); West End (10/98); and Torqua Springs (10/98). San Clemente Island: Northwest Harbor (5/98); Dune Point (5/98, 9/98); Pyramid Cove (5/98, 9/98); Pyramid Head (5/98, 9/98); and Seal Cove (9/98). Santa Barbara Island: Southeast Sea Lion (9/98: most recruits ever); Arch Point (9/98: most recruits ever); and Cat Canyon (33° 27.24′ N, 119° 02.47′ W) (9/98). Anacapa Island: Survey Rock (6/98); Frenchy's Cove (6/98); Landing Cove (8/98: most recruits ever (4.1/ARM)), 8/99 (2.3/ARM); Cathedral Cove (7/98: most recruits ever (1.8/ARM)), 7/99 (0.5/ARM); and Admiral's Reef (8/98: most recruits ever (4.4/ARM)), 8/99 (2.5/ARM). Santa Cruz Island: Gull Island (8/98: first recruits ever (0.7/ARM), 9/99 (1.0/ARM); Fry's Harbor (7/98: most recruits ever (0.6/ARM), 8/99 (0.4/ARM); Pelican Bay (8/98: most recruits ever (2.7/ARM), 8/99 (0.2/ARM); Scorpion Cove (8/98 (0.17/ARM); Yellowbanks (9/98: first recruits ever (0.9/ARM), 7/99 (1.9/ARM); and Potato Rock (8/98). No *Centrostephanus* <20 mm were found in ARMs in 2000. Two coronado urchins (7/99 (25 mm), 8/00) found on a transect at Rodes Reef became the first record of this species at Santa Rosa Island.

Remarks.—The huge settlement of *Centrostephanus* in late 1997/early 1998 also was observed in San Diego (Mission Bay Reef); numbers of tiny urchins dropped substantially by late 1998 (C. Gramlich pers. comm.).

Discussion

Six species of subtropical nearshore invertebrates were documented for the first time in California. New northern geographic range limits based on records at the Channel Islands include the following: 1) *Chloeia viridis*: extended from Gulf of California to Santa Catalina Island; 2) *Stenorhynchus debilis*: extended from Guadalupe Island to Anacapa Island; 3) *Pleurobranchus areolatus*: extended from San Benitos Islands to Anacapa Island; 4) *Chromodoris galexorum*: extended from Guadalupe Island to Santa Catalina Island; 5) *Polycera alabe*: extended from Cedros Island to Anacapa Island; and 6) *Holothuria impatiens*: extended from Rosario Bay to Santa Catalina Island.

Six additional species of subtropical invertebrates, though occurring within or near their known geographic range limits, were documented for the first time at one or more of the Channel Islands during or after the 1997–1998 El Niño period. New island records include: 1) *Bunodactis* sp.: previously reported at Mission Bay, now known at San Clemente and Santa Catalina Islands; 2) *Hemisquilla ensigera californiensis*: increased abundances at four islands and newly appeared near the west end of Santa Cruz Island; 3) *Dromidia larraburei*: first island record at Anacapa Island; 4) *Pteria sterna*: newly found at three northern islands; 5) *Arbacia incisa*: previously reported from Newport Bay, now known at five islands; and 6) *Centrostephanus coronatus*: increased recruitment at six islands and newly appeared at Santa Rosa Island.

The conspicuousness of most of the above invertebrates coupled with extensive CIRP and CINP surveys dating back to 1980 make it unlikely that these warm-water species would have occurred at the newly-recorded island locations prior to the 1997–1998 El Niño without being noticed. The observed temporal pattern of predominantly smaller individuals during El Niño followed by larger sizes during La Niña for *Stenorhynchus, Hemisquilla, Pteria, Arbacia,* and *Centrostephanus* is consistent with the hypothesis that their larvae settled out from El Niño-associated currents flowing north from Baja California (see Hickey 1993). Previous northern limits for some of these species (e.g., *Stenorhynchus, Pleurobranchus, Chromodoris,* and *Polycera*) were established after El Niño events of the 1980's. Such progressive extensions of northern range limits are likely a result of the extended warm-water regime in place since 1976 (Engle 1994).

Long-term sea surface temperature patterns show consistent differences among the eight Channel Islands (Fig. 1). Santa Catalina, the warmest island, had the most records of subtropical invertebrates (Table 1), as well as subtropical fishes (see Richards and Engle this volume). Another warm-water island, San Clemente, and a transitional island, Anacapa, also had many southern species records. Though more northern, Anacapa Island is close to the mainland where it is influenced by northerly-flowing warm-water currents. The few subtropical species records at Santa Barbara Island may be due to its paucity of sheltered habitats (where at least 5 of the species were found) and because this island was surveyed less often than Santa Catalina, San Clemente, and Anacapa. Remote, military-controlled San Nicolas Island was only surveyed at two locations in September 1999. The northern islands within Channel Islands National Park were visited regularly. Only two minor occurrences of subtropical species were noted at Santa Rosa Island and none at San Miguel, the coldest-water island.

Repeated sightings provided growth and survivorship information for five species. Short-lived *Stenorhynchus* was found only during an eight-month period in 1998. Aquarium-held individuals also died by fall 1998. In contrast, *Arbacia,* found as 8–10 mm juveniles in spring 1998, continued to be found as adults in 1999 and 2000. All three aquarium-held *Arbacia* survived for over two years (as of 9/2000), having grown from an average of 9 mm to 32 mm test diameter. *Pteria* was found in progressively larger sizes at many sites over the two-year period from fall 1998 to fall 2000, with many empty shells evident in 2000. The lack of small *Stenorhynchus, Arbacia,* or *Pteria* in the two years following the 1997/1998 settlement indicates that these populations are not likely self-sustaining. As has often been observed in populations at their northern limits (e.g., Reaka 1986), these species (as well as *Chloeia, Pleurobranchus,* and *Chromodoris*) attained or exceeded maximum recorded sizes. *Hemisquilla* and *Centrostephanus* also experienced El Niño recruitment peaks. Their established populations on southern islands may make it easier for further recruitment to northern islands.

The 1997–1998 El Niño influenced the composition of Channel Islands shallow-water species assemblages in many other ways besides the enhancement of subtropical species (see Tegner and Dayton 1987 for 1983–1984 El Niño effects). For example, certain herbivores, planktivores, and seastars, incurred high mortality apparently due to thermal stress, reduced food availability, and disease (J.

Engle and D. Richards, unpub. data). Deterioration of kelp forests reduced habitat, shelter, and food for many species. Low oceanographic productivity resulted in less food for suspension-feeders. Seastars and other echinoderms experienced extensive mortality from a warm-water wasting disease (Eckert et al. 2000). The rapid switch from El Niño to La Niña conditions in fall 1998 reversed thermal stress, low productivity, and echinoderm disease influences. Also, La Niña apparently halted further recruitment of subtropical forms, but did not appear to affect the survival of the subtropical species we monitored. It remains to be seen whether this La Niña signals the start of an oceanographic regime shift toward cooler conditions or is a temporary deviation in the long-term warming trend. If warm-water conditions resume, we can expect further appearances of subtropical species at the Channel Islands as biogeographic provinces shift northward.

Acknowledgments

Many individuals participated in the surveys that provided new records for subtropical invertebrates at the Channel Islands. We thank the Channel Islands Research Program and Channel Islands National Park research vessel crews and divers for their assistance, especially David Kushner for directing the CINP Kelp Forest Monitoring Program surveys. We thank Erik Erikson, Constance Gramlich, Pete Haaker, and Loretta Roberson for providing additional records of unusual invertebrates. We greatly appreciate the underwater photographic talents of Jay Carroll, Erik Erikson, Richard Herrmann, and Loretta Roberson. Valuable taxonomic and biogeographic expertise were provided by Dave Behrens, Don Cadien, Henry Chaney, Dan Gotshall, Leslie Harris, Gordon Hendler, John Ljubenkov, Paul Valentich Scott, and Mary Wicksten. The surveys were sponsored by the Tatman Foundation (CIRP) and National Park Service (CINP).

Literature Cited

Basch, L. V. and J. M. Engle. 1989. Aspects of the ecology and behavior of the stomatopod *Hemisquilla ensigera californiensis* (Gonodactyloidea: Hemisquillidae). Pp. 199–212 *in* Biology of stomatopods (E. A. Ferrero, ed.), Sel. Symp. Monogr. U.Z.I., 3, Mucchi, Modena.

Basch, L. V. and J. M. Engle. 1993. Biogeography of *Hemisquilla ensigera californiensis* (Crustacea: Stomatopoda) with emphasis on Southern California Bight populations. Pp. 211-220 *in* Third California Islands symposium: recent advances in research on the California Islands (F.G. Hochberg, ed.), Santa Barbara Museum of Natural History, xiii + 661 pp.

Behrens, D. W. 1991. Pacific Coast nudibranchs. Sea Challengers, vi + 107 pp.

Bertsch, H. 1978. The Chromodoridinae nudibranchs from the Pacific Coast of America. Pt. II. The genus *Chromodoris*. Veliger 20(4):307–327.

Bertsch, H. and A. N. Kerstich. 1984. Distribution and radular morphology of various nudibranchs (Gastropoda: Opisthobranchia) from the Gulf of California. Veliger 26(4):264–273.

Brusca, R. C. 1980. Common intertidal invertebrates of the Gulf of California. University of Arizona Press, xx + 513 pp.

Clark, H. L. 1948. A report on the echini of the warmer eastern Pacific based on the collections of the Velero III. Allan Hancock Pacific Exped. 8:225–352.

Coan, E. V., P. V. Scott, and F. R. Bernard. 2000. Bivalve seashells of western North America. Santa Barbara Museum of Natural History Monographs No. 2, vii + 764 pp.

CoastWatch Bulletins. 1997–2000. West Coast Regional Node, National Oceanic and Atmospheric Administration, Southwest Fisheries Science Center. La Jolla, California.

Collier, C. L., and W. M. Farmer. 1964. Additions to the nudibranch fauna of the east Pacific and the Gulf of California. Trans. San Diego Soc. Nat. Hist. 13(19):377–396.

Davis, G. E., D. J. Kushner, J. M. Mondragon, J. E. Morgan, D. Lerma, and D. Richards. 1999. Kelp forest monitoring handbook, Vol. 1: Sampling Protocol. Channel Islands National Park. 55 pp.

Eckert, G. L., J. M. Engle, and D. J. Kushner. 2000. Sea star disease and population declines at the Channel Islands. Pp. 390–393 *in* Proceedings of the fifth California Islands symposium (D. R. Browne, K. L. Mitchell, and H. W. Chaney, eds.), U. S. Minerals Management Service.

Engle, J. M. 1993. Distributional patterns of rocky subtidal fishes around the California Islands. Pp. 475–484 *in* Third California Islands symposium: recent advances in research on the California Islands (F. G. Hochberg, ed.), Santa Barbara Museum of Natural History, xiii + 661 pp.

Engle, J. M. 1994. Structure and dynamics of nearshore marine assemblages of the California Channel Islands. Pp. 13–26 *in* Fourth California Islands symposium: update on the status of resources (W. L. Halvorson and G. J. Maender, eds), Santa Barbara Museum of Natural History, 530 pp.

Gotshall, D. W. 1994. Guide to marine invertebrates: Alaska to Baja California. Sea Challengers, vi + 105 pp.

Gotshall, D. W. 1998. Sea of Cortez marine animals. Sea Challengers, v + 110 pp.

Hartman, O. 1940. Polychaetous annelids. Pt. 2. Chrysopetalidae to Goniadidae. Allan Hancock Pac. Exped. 7(3):173–287.

Hendler, G., J. E. Miller, D. L. Pawson, and P. M. Kier. 1995. Sea stars, sea urchins, and allies: echinoderms of Florida and the Caribbean. Smithsonian Institution Press, xi + 390 pp.

Hickey, B. M., 1993. Physical oceanography. Pp. 19–70 *in* Ecology of the Southern California Bight (M.D. Dailey, D.J. Reish, and J.W. Anderson, eds.), University of California Press, xvi + 926 pp.

Jensen, G. C. 1995. Pacific Coast crabs and shrimps. Sea Challengers, viii + 87 pp.

Keen, A. M. 1971. Sea shells of Tropical West America. Stanford University Press, xiv + 1064 pp.

Kerstitch, A. N. 1989. Sea of Cortez marine invertebrates. Sea Challengers, v + 114 pp.

Kushner, D. J., D. Lerma, S. Alesandrini, and J. Shaffer. 1999. Kelp forest monitoring annual report 1998. Channel Islands National Park, 68 pp. + appendices.

Ljubenkov, J. 1995. A new species of stinging anemone from southern California and the Gulf of California. Western Society of Naturalists 76th Annual Meeting Abstract.

McPhaden, Michael J. 1999. Genesis and evolution of the 1997–98 El Niño. Science 283:950–954.

Montagne, D. E. and D. B. Cadien. 2001. Northern range extensions into the Southern California Bight of ten decapod crustacea related to the 1991/92 and 1997/98 El Niño events. Bull So. Cal. Acad. Sci., 100: 199–211.

Morris, R. H., D. P. Abbott, and E. C. Haderlie, eds. 1980. Intertidal invertebrates of California. Stanford Univ. Press, ix + 690 pp.

Radovitch, J. 1961. Relationships of some marine organisms of the northeast Pacific to water temperatures. Calif. Dept. Fish and Game Fish Bull. No. 112, 62 pp.

Reaka, M. L. 1986. Biogeographic patterns of body size in stomatopod Crustacea: Ecological and evolutionary consequences. Pp. 209–235 *in* Crustacean Issues, Vol. 4 (R. Gore and K. Heck, eds.), Balkema Press, Rotterdam.

Richards, D. V., and J. M. Engle. 2001. New and unusual reef fish discovered at the California Channel Islands during the 1997-1998 El Niño. Bull. So. Cal. Acad. Sci., 100: 175–185.

Schmitt, W. L. 1921. The marine decapod crustacea of California. Univ. Calif. Publ. Zool. 23:1–470.

Sewell, A. T., and S. L. Williams. 1995. The negative effects of anemone epiphytes on eelgrass in an urban estuary. Western Society of Naturalists 76th Annual Meeting Abstract.

Strachan, A. R., C. H. Turner, and C. T. Mitchell. 1968. Two fishes and a mollusk, new to California's marine fauna, with recent comments regarding other recent anomalous occurrences. Calif. Dept. of Fish and Game Fish Bull. 54(1): 49–57.

Tegner, M. J., and P. K. Dayton. 1987. El Niño effects on Southern California kelp forest communities. Adv. Ecol. Res. 17:243–279.

Accepted for publication 22 December 2000.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 199–211

Northern Range Extensions into the Southern California Bight of Ten Decapod Crustacea Related to the 1991/92 and 1997/98 El Niño Events

David E. Montagne[1] and Donald B. Cadien[2]

[1]*Ocean Monitoring & Research, County Sanitation Districts of Los Angeles County, 1955 Workman Mill Road, Whittier, California 90601*
[2]*Marine Biology Laboratory, County Sanitation Districts of Los Angeles County, 24501 S. Figueroa Street, Carson, California 90745*

Abstract.—The first recorded appearance in the Southern California Bight (SCB) of ten decapod crustaceans, all of which have distributions that are primarily tropical or sub-tropical, is documented. Northern range extensions are provided for the penaeidean shrimp *Metapenaeopsis mineri* (Penaeidae) and *Sicyonia penicillata* (Sicyoniidae), the caridean shrimp *Processa peruviana* (Processidae), *Pantomus affinis, Plesionika beebei, P. trispinus,* and *P. carinirostris* (Pandalidae) and the brachyuran crabs *Stenorhynchus debilis* (Majidae), *Palicus cortezi,* and *P. lucasii* (Palicidae). These animals were collected during or in the aftermath of the 1991/92 and 1997/98 El Niño events. The specimens were collected in trawl monitoring programs of shelf and upper slope depths that have been in place for up to three decades. These long term data sets provide evidence of previous absence from the SCB, accentuating the novelty of these records.

The warm temperate waters of the Southern California Bight (SCB) are known as a transitional area between the cool temperate fauna to the north and the tropical faunas to the south (e.g., the Oregonian vs. Mexican and Panamanian regions of Briggs 1974). They have been treated as a semi-discrete zoogeographic entity, the Californian Transition Zone (Newman 1979). The northern limit of many species with primarily tropical or subtropical distributions often falls within the SCB. The dominance of the northerly flowing California Countercurrent and California Undercurrent within the Bight (Hickey 1993) and the barrier presented to southern species by the California Current north of Pt. Conception are the primary physical determinants of this pattern. In addition, large-scale and interdecadal cycles of warming seawater temperatures (McGowan *et al.* 1998) are accompanied by shifts in the Bight fauna as cool temperate species decline and warm temperate species are favored (Stephens *et al.* 1988; Love *et al.* 1998). Superimposed on these cycles is the El Niño/Southern Oscillation (ENSO), warm water (El Niño) and cold water (La Niña) events that occur on a cycle of four to ten years with varying intensity. When intense, an El Niño may be accompanied by striking incursions into the SCB of species whose center of distribution lies well to the south (Radovich 1961; Mearns 1988; Lea & McAlary 1994; Martin & Velarde 1997). These factors contribute to the distinctive and variable nature of the SCB fauna. This paper documents the first recorded appearance in the SCB of ten decapod crustaceans, all of which have distributions that are primarily tropical, subtropical, or Cortezian. All but two of these animals were collected during the 1997/98 El Niño period and its immediate aftermath. The remaining two species were taken during or immediately after the 1991/92 El Niño.

All specimens reported here were collected during shelf and upper slope depth otter trawl surveys of demersal fish and epibenthic invertebrates. The surveys include those conducted as part of wastewater impact monitoring programs performed by the County Sanitation Districts of Los Angeles County (CSDLAC), the Orange County Sanitation District (OCSD) and the City of San Diego Metropolitan Wastewater Department (CSDMWWD). Other material was collected during powerplant monitoring in Long Beach Harbor by MBC Applied Environmental Sciences or during the Southern California Bight 1998 Regional Monitoring Program (Bight'98), a large scale, multi-agency regional survey of the SCB carried out during July and August of 1998. Most of these specimens are retained as vouchers or reference specimens by the capture agencies. In some cases specimens have been deposited in the Crustacea collection of the Natural History Museum of Los Angeles County. All are available for inspection, regardless of their repository.

Order Decapoda
Suborder Dendrobranchiata
Infraorder Penaeidea
Superfamily Penaeoidea
Family Penaeidae

Metapenaeopsis mineri Burkenroad, 1934

Metapenaeopsis mineri Burkenroad, 1934:25, Figs. 9, 10 [in part]
Metapenaeopsis mineri: Hendrickx, 1996:23–26, Figs. 11 a, b, c, & 12

Type locality.—Bahía Concepción, Baja California Sur, Mexico.

Material examined.—Off the mouth of the Tijuana River, California: 1 specimen, CSDMWWD Station SD-18 (32°32.52′N, 118°11.357′W), 32 m depth, 26 January 1998.

Remarks.—This is a range extension along the Pacific Coast of approximately 8° of latitude. Species of *Metapenaeopsis* are generally similar in body form to, but much smaller than, species of *Farfantepenaeus* with which they co-occur. It is possible that, if not closely examined, they are sometimes mistaken in the field for juveniles of the larger species. The genera are distinguished by the presence of ventral rostral teeth in *Farfantepenaeus.*

Distribution.—Off the mouth of the Tijuana River, California, USA (this paper); Bahía Magdalena, Baja California Sur, Mexico and throughout the Gulf of California (Hendrickx 1996) at depths of 13 to 115 m.

Family Sicyoniidae

Sicyonia penicillata Lockington, 1879
Figure 1

Sicyonia penicillata Lockington, 1879: 164
Eusicyonia penicillata: Burkenroad, 1934: 88, Figs. 30, 31, 33
Sicyonia penicillata: Hendrickx, 1984: 285, Figs. 6, 20, 26
Sicyonia penicillata: Pérez Farfante, 1985: 38–43, Figs. 31–34
Sicyonia penicillata: Hendrickx, 1996:109–113, Figs. 56 a, b, c, 57

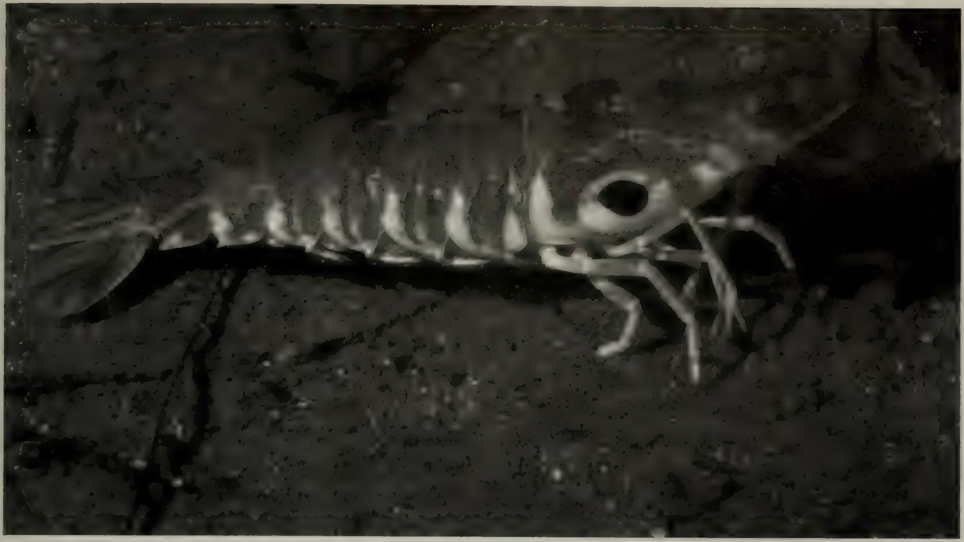


Fig. 1. *Sicyonia penicillata.* Specimen photographed at the head of Redondo Submarine Canyon, approx. 20 m depth, 6 June 1999. Photo by Mr. Ken Kurtis.

Type locality.—Bolinas Bay [suspected to be Bahía de Ballenas by Hendrickx 1996], Baja California Sur, Mexico, 26 m depth.

Material examined.—Off the Palos Verdes Peninsula, California: 2 specimens, CSDLAC Station T0-61 (33°48.57′N, 118°25.84′W), 61 m depth, 18 February 1998. 1 specimen, CSDLAC Station T0-23 (33°48.19′N, 118°25.04′W), 23 m depth, 20 May 1998. Back Channel, Long Beach Harbor, California: 1 specimen, Long Beach Generating Station Monitoring Program Station T10 (33°45.30′N, 118°13.00′W), 18 m depth, 12 August 1988. Off Huntington Beach, California: 1 specimen, OCSD Station T11 (33°36.06′N, 118°05.20′W), 56 m depth, 10 January 2000. 1 specimen, OCSD Station T13 (33°35.54′N, 118°03.64′W), 56 m depth, 10 January 2000. Off Torrey Pines State Beach, California: 1 specimen, Bight'98 Station 2349 (32°53.604′N, 117°16.118′W), 32 m depth, 6 August 1998.

Remarks.—This is a range extension along the Pacific coast of approximately 4° of latitude. The well-developed carapace marking readily distinguishes this species from *Sicyonia ingentis,* the common species in the SCB. Even so, the collection of the species in Long Beach Harbor in the aftermath of the 1986/87 El Niño went undocumented in the literature until now. A photograph of *Sicyonia penicillata* was taken by Mr. Ken Kurtis while diving at the head of the Redondo Submarine Canyon and is included with his permission (Fig. 1). The photograph was taken at night on 6 June 1999 in approximately 20 m depth. It illustrates the distinctive carapace spot of this species, although in most specimens examined by the authors the central field of the spot is lighter in color, contrasting with its margins. The latitude at the head of the canyon is approximately 33°50′N. Mr. Kurtis also reports seeing other *S. penicillata* in the area of the canyon around this time as shallow as 5 m. Word and Charwat (1976) treat this species, but do not provide records from Southern California Bight waters.

Distribution.—Off Palos Verdes, California, USA (this paper); southeast of Punta Canoas, Baja California Norte to Bahía San Lucas, Baja California Sur, Mexico and throughout the Gulf of California (Hendrickx 1996); off Puntarenas, Costa Rica (Pérez Farafante 1985) at depths of 1 to 180 m.

Suborder Pleocyemata
Infraorder Caridea
Superfamily Processoidea
Family Processidae

Processa peruviana Wicksten, 1983

Processa peruviana Wicksten, 1983: 29–30, Figs. 4–6
Processa sp.: Méndez, 1981: 98, Fig. 294

Type locality.—Isla Manuelita, Costa Rica: 1 specimen, *Velero IV* Station 19044 (5°36′09″N, 87°01′14″W), 146 m depth, 3 June 1973.

Material examined.—Off the Palos Verdes Peninsula, California: 1 specimen, near CSDLAC Station T0-61 (33°48.57′N, 118°25.84′W), 50 m depth, 8 November 1995. Off Point Loma, California: 1 specimen, CSDMWWD Station B11 (33°46.57′N, 117°21.35′W), 89 m depth, 13 July 1999.

Remarks.—Wicksten (1983) indicates this species frequents sandy bottoms. Locally collected individuals have also come from sites where the sea-floor was sandy rather than rocky or muddy. Both specimens taken in the Southern California Bight were gravid females, and it is likely that the species is reproductive at the northern limit of its range. No juveniles have yet been taken in the area, however, suggesting that recruitments are unsuccessful.

Distribution.—Off Palos Verdes, California, USA (this paper); Isla San Benito, outer coast of Baja California to Máncora, Perú (Wicksten 1983), throughout the Gulf of California and the Galapagos (Wicksten & Hendrickx 1992) at depths of 11 to 180 m.

Superfamily Pandaloidea
Family Pandalidae

Pantomus affinis Chace, 1937

Pantomus affinis Chace, 1937:116–118, Fig. 3
Pantomus affinis: Hendrickx & Wicksten, 1989: 73–75, Fig. 1

Type locality.—Santa Inez Bay, Baja California, Mexico: 65 specimens, Station 147 D-2 (26°56′30″N, 111°48′30″W), 110 m depth, 17 April 1936.

Material examined.—Off Point Dume, California: 1 specimen, Bight'98 Station 2116 (33°58.878′N, 118°42.530′W), 191 m depth, 19 August 1998. Off the Palos Verdes Peninsula, California: 12 specimens, CSDLAC Station T0-137 (33°48.83′N, 118°26.36′W), 140 m depth, 5 November 1997. 1 specimen, CSDLAC Station T4-137 (33°42.06′N, 118°21.05′W), 140 m depth, 19 May 1998. 4 specimens, CSDLAC Station T5-137 (33°41.11′N, 118°19.61′W), 140 m depth, 19 May 1998. 1,132 specimens, CSDLAC Station T0-137 (33°48.83′N, 118°26.36′W), 140 m depth, 5 August 1998. 2 specimens, CSDLAC Station T0-305 (33°49.23′N, 118°27.09′W), 305 m depth, 5 August 1998. 331 specimens, CSDLAC Station T0-137 (33°48.83′N, 118°26.36′W), 140 m depth, 6 November 1998. 280 specimens, CSDLAC Station T0-137 (33°48.83′N, 118°26.36′W), 140 m depth, 12 February 1999. 150 specimens, CSDLAC Station T0-137

(33°48.83′N, 118°26.36′W), 140 m depth, 13 May 1999. Off Newport Beach, California: 3 specimens, Bight'98 Station 2119 (33°34.736′N, 117°55.184′W), 117 m depth, 7 August 1998. Santa Catalina Island, California, off West End: 2 specimens, Bight'98 Station 2065 (33°29.494′N, 118°34.708′W), 199 m depth, 21 July 1998. Off Imperial Beach, California: 1 specimen, CSDMWWD Station SD-7 (32°35.06′N, 117°18.39′W) 98 m depth, 25 January 1993. 6 specimens, CSDMWWD Station SD-7 (32°35.06′N, 117°18.39′W) 98 m depth, 23 January 1998.

Remarks.—Gravid females were common in the catches. The large collection on 5 August 1998 (1,132 specimens) included many gravid females with eggs in varying stages of development up to the eyed stage. Approximately 17% of the shrimp in this collection were gravid females. This is a range extension of *Pantomus affinis* along the Pacific Coast of approximately 8° of latitude. The population established around the Redondo and Santa Monica Submarine Canyons has not been seen since May of 1999 and may no longer exist; the last collection of *P. affinis* in the San Diego region was in April 1999 (R. Velarde, pers. com.).

A number of specimens of *Pantomus affinis* bore parasitic isopods of the genus *Zonophryxus* (Family Dajidae) on their carapaces. The species appears to be undescribed, but original descriptions in this group are lacking in detail, and type material must be reexamined to determine the status of several described species. Larger *Zonophryxus* specimens were also seen on *Plesionika trispinus* collected in the same locale (*q.v.*). They seem to belong to the same species as the smaller individuals found on *Pantomus*. The range of the parasite is not known; no described members of the genus have been reported from within 20° of latitude either north or south of the present captures. They have not been observed on southern populations of *Pantomus* or *Plesionika trispinus* (M. E. Hendrickx, pers. com.).

Distribution.—Point Dume, California, USA (this paper); Bahía Santa Inés, Gulf of California, Baja California Sur, and Bahía de Santa Maria, Sinaloa, Mexico to Isla Lobos de Tierra, Perú (Hendrickx & Wicksten 1989) at depths of 35 to 744 m.

Plesionika beebei Chace, 1937

Plesionika beebei Chace, 1937:114, Fig. 2
Plesionika beebei: Hendrickx & Wicksten, 1989:76–77, Figs. 4, 5
Plesionika beebei: Hendrickx & Estrada Navarrete, 1996:131–132, Figs. 80, 81

Type locality.—Gulf of California, Baja California Sur, Mexico (26°48′N, 111°20′W).

Material examined.—Off the Palos Verdes Peninsula, California: 1 specimen, CSDLAC Station T5-305 (33°40.85′N, 118°19.85′W), 305 m depth, 6 November 1997.

Remarks.—This is a range extension along the Pacific Coast of approximately 8° of latitude.

Distribution.—Palos Verdes Peninsula, California, USA (this paper); off Punta Tosca, Baja California Sur, and off Guaymas, Sonora, Gulf of California, Mexico to Máncora Bank, Perú (Hendrickx & Wicksten 1989) at depths of 73 to 738 m.

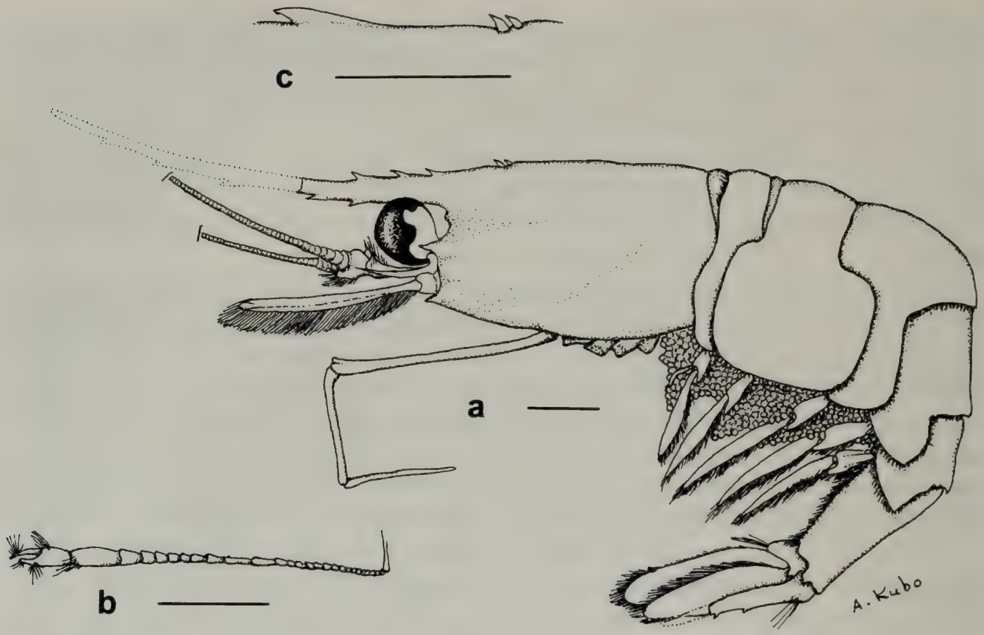


Fig. 2. *Plesionika carinirostris,* scale bars = 5 mm. a, Lateral perspective, the rostrum, lost subsequent to collection, is illustrated with dashed lines. All but 1st pereopod detached from specimen and not figured. b, 2nd pereopod, illustrating the subdivision of the carpus into 26 articles. c, Dorsal, movable carapace spines.

Plesionika carinirostris Hendrickx, 1990
Figure 2 a, b, c

Plesionika carinirostris Hendrickx, 1990:38–39, Figs. 2, 3
Plesionika carinirostris: Hendrickx, 1995:481

Type locality.—Off Isla San Lorenzo, Gulf of California, Mexico.

Material examined.—Off the Palos Verdes Peninsula, California, in the north arm of the San Pedro Sea Valley: 1 specimen, CSDLAC Station V150 (33°39.429′N, 118°17.325′W), 145 m depth, 29 June 1999.

Remarks.—*Plesionika carinirostris* was previously known only from the type material, a single male collected in the central Gulf of California. While Hendrickx (1995) lists the holotype as a female (hembra), the type description clearly indicates it as male. The new record off Palos Verdes suggests a range through the southern Gulf of California and along the Pacific Coast of Baja California. Hendrickx (1990, 1995) remarks on the large size of the type specimen (110 mm total length, 21 mm carapace length). The Palos Verdes specimen is a gravid female and also of large size. Since the rostrum was broken before measurement, the total length is estimated at 122 mm (25 mm carapace length). The color in life, previously undescribed, is dull scarlet blotches on a translucent white ground. The antennae are solid scarlet, while the remaining appendages are nearly all white, without contrasting color on the legs. The entire oral field of the animal is bright scarlet, the remainder of the ventrum unpigmented. The egg mass is lavender.

Distribution.—Palos Verdes Peninsula, California, USA, at a depth of 150 m (this paper); Central Gulf of California (near Isla San Lorenzo), Mexico at between 360–380 m depth (Hendrickx 1990).

Plesionika trispinus Squires & Barragán, 1976

Plesionika trispinus Squires & Barragán, 1976:113–117, Figs. 1, 2
Plesionika trispinus: Hendrickx & Wicksten, 1989:80–81, Figs. 4, 5
Plesionika trispinus: Hendrickx & Estrada Navarette, 1996:134–136, Figs. 83, 84

Type locality.—Off Pizarro, Columbia.

Material examined.—Off the Palos Verdes Peninsula, California: 6 specimens, CSDLAC Station T4-137 (33°42.06′N, 118°21.05′W), 140 m depth, 17 February 1998. 4 specimens, CSDLAC Station T5-137 (33°41.11′N, 118°19.61′W), 140 m depth, 17 February 1998. 2 specimens, CSDLAC Station T4-137 (33°42.06′N, 118°21.05′W), 140 m depth, 19 May 1998. 2 specimens, CSDLAC Station T1-137 (33°43.84′N, 118°25.34′W), 140 m depth, 4 August 1998. 1 specimen, CSDLAC Station T0-305 (33°9.23′N, 118°27.09′W), 305 m depth, 5 August 1998. 1 specimen, CSDLAC Station T1-305 (33°43.55′N, 118°25.64′W), 305 m depth, 6 August 1998. 2 specimens, CSDLAC Station T5-305 (33°40.85′N, 118°19.85′W), 305 m depth, 6 August 1998. 1 specimen, CSDLAC Station T0-305 (33°49.23′N, 118°27.09′W), 305 m depth, 11 August 1999. Off Newport Beach, California: 3 specimens, Bight'98 trawl Station 2119 (33°34.74′N, 117°55.18′W), 194 m depth, 7 August 1998.

Remarks.—A parasitic dajid isopod of the genus *Zonophryxus* was taken on several *Plesionika trispinus.* They seem to be larger individuals of the same species found on *Pantomus affinis* in the area (*q.v.*). As the host is larger, the parasite can attain larger sizes, although reproductively mature even on the smaller host. Use of multiple hosts is unusual, but not unprecedented in the Dajidae (Koehler 1911; Brandt 1993). This is a range extension along the Pacific Coast of approximately 9° latitude for this shrimp. The range of the parasite is unknown.

Distribution.—Palos Verdes Peninsula, California, USA (this paper); Bahía de Santa Maria, Sinaloa, Mexico to off Salaverry, Perú (Hendrickx & Wicksten 1989) at depths of 96 to 500 m.

Suborder Reptantia
Infraorder Brachyura
Superfamily Oxyrhyncha
Family Majidae

Stenorhynchus debilis (Smith, 1871)

Leptopodia debilis Smith, 1871: 87
Stenorhynchus debilis: Rathbun, 1898: 568

Type locality.—Povlon, Bay of Realejo (Corinto), Nicaragua: 1 specimen, male, No. 3948, Museum of Comparative Zoology, Harvard.

Material examined.—Off Huntington Beach: 1 specimen, OCSD Station T11 (33°36.06′N, 118°05.20′W), 60 m depth, 11 August 1999. Santa Catalina Island, California, White Cove: 1 specimen, Bight'98 Station 2077 (33°23.75′N, 118°21.84′W), 50 m depth, 22 July 1998. West of Salta Verde Point: 1 specimen,

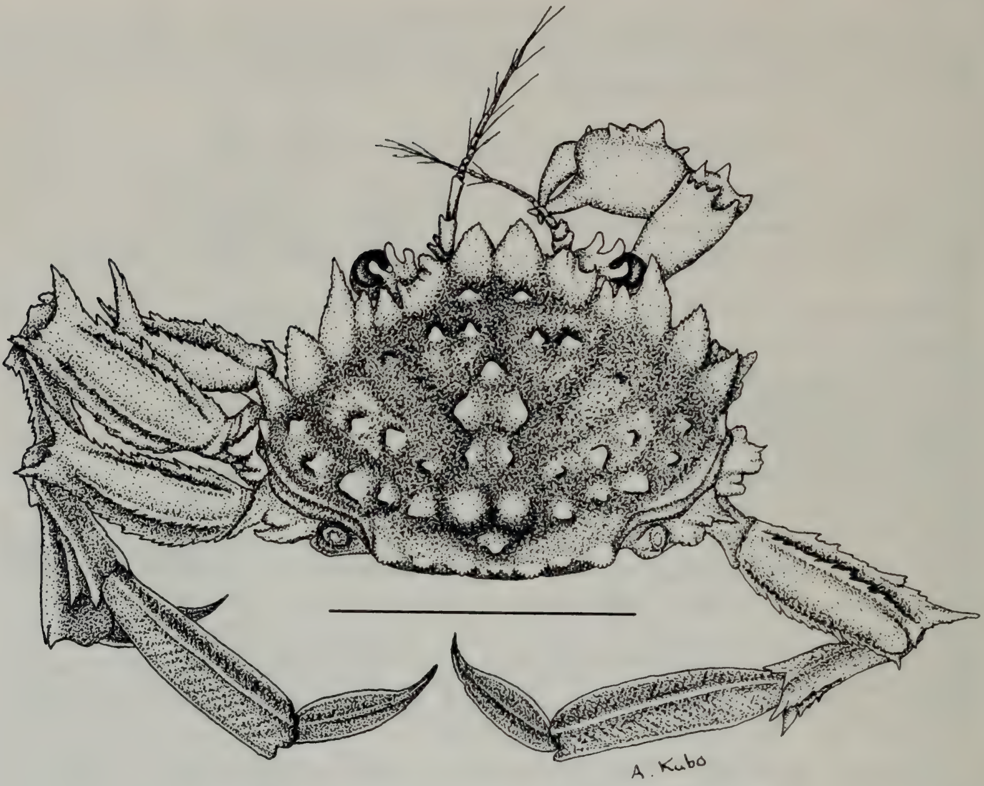


Fig. 3. *Palicus cortezi,* dorsal view, scale bar = 10 mm.

Bight'98 Station 2087 (33°18.57′N, 118°26.76′W), 69 m depth, 24 July 1998. Off the Palisades: 1 specimen, Bight'98 Station 2116 (33°18.34′N, 118°21.91′W), 39 m depth, 24 July 1998.

Remarks.—In addition to the trawl-caught material examined by the authors, reports of *Stenorhynchus debilis* were common and widespread at diving depths in the central SCB during 1998 (*e.g.* Engle & Richards, this volume).

Distribution.—Huntington Beach, California, USA (this paper); Bahía Magdalena, Baja California Sur, Mexico, throughout the Gulf of California to Valpariso, Chile; Guadalupe Island, Rocas Alijos, Revillagigedo, Cocos, and Galapagos islands (Hendrickx 1999) at depths of 3 to 156 m.

Superfamily Ocypodoidea
Family Palicidae

Palicus cortezi (Crane, 1937)
Figure 3

Cymopolia cortezi Crane, 1937: 75–76; Plate VIII, Fig. 25
Cymopolia cortezi: Garth, 1946: 499–500; Plate 85, Fig. 2

Type locality.—Santa Inez Bay, Gulf of California: 1 specimen, Department of Tropical Research of the New York Zoological Society Station 147, Dredge 2, (26°57.5′N, 111°48.5′W), 120 m depth, 17 April 1936.

Material examined.—Off the Palos Verdes Peninsula, California: 1 specimen, CSDLAC Station T0-61 (33°48.57′N, 118°25.84′W), 61 m depth, 23 February 1994.

Remarks.—This is a range extension of approximately 7° of latitude, although the shoreline distance between the two sites is much greater than 420 miles. This specimen, like the holotype a male, was initially identified as *P. lucasii.* Examination by Mr. Todd Zimmerman (NHMLAC) corrected this based on the form of the pleopod. Aside from the formation of the anterior carapace and the male pleopods, the two species are quite similar. While several palicids are known from the Panamic region, this and the following species are the first members of the family reported from the Pacific Coast of the United States.

Distribution.—Palos Verdes, California, USA (this paper); Santa Inez Bay, Gulf of California, Mexico; Wenman Island, Galapagos at depths of 61–300 m (Garth, 1946).

Palicus lucasii Rathbun, 1898

Palicus lucasii Rathbun, 1898: 600, Pl. 43, Fig. 2
Cymopolia lucasii: Rathbun, 1918: 193–194, Pl. 44, Fig. 1, 2
Cymopolia lucasii: Crane, 1937: 76
Cymopolia lucasii: Garth, 1946: 500–501, Plate 87, Fig. 1

Type locality.—Off Cabo San Lucas, Baja California Sur, Mexico; 7 specimens, Albatross Station 2829, (22°52′00′N, 109°55′00″W), 57 m depth, 1 May 1888.

Material examined.—Off Imperial Beach, California: 1 specimen, CSDMWWD Regional Station 2101 (33°48.57′N, 118°25.84′W), 38 m depth, 30 July 1996.

Remarks.—This is a range extension of approximately 10° of latitude. This specimen, a male, was examined by Mr. Todd Zimmerman (NHMLAC) along with the specimen of *P. cortezi* mentioned above. The form of the male pleopod in this specimen was essentially the same as that seen in specimens in Zimmerman's collection from several other sites.

Distribution.—Imperial Beach, California, USA (this paper); Cabo San Miguel, Baja California (Hendrickx & Salgado Barragán 1997); mid to lower Gulf of California (Hendrickx 1994), Clarion Island (Hendrickx 1992), and Albemarle, Hood, and James Islands, Galapagos (Garth 1946) at depths of 20–120 m.

Discussion

The use of otter trawls as a means surveying shelf and slope depth communities has been a common element of marine monitoring programs in the SCB since the 1970s. Most of this effort has been directed at monitoring the effects of treated wastewater discharged from large sanitary outfalls located along the metropolitan coastline between Los Angeles and San Diego. While these programs are local, being focused on the receiving water area within the effect of a discharge, they are of long duration and regular frequency. For example, CSDLAC has been conducting semiannual or quarterly trawls at 16 to 22 sites on the Palos Verdes shelf and upper slope in depths of 25 to 300 m since 1972. Over 1500 trawls have been conducted as part of that ongoing effort. The City of Los Angeles, the OCSD, and the City of San Diego have been conducting similar long term surveys as well. In addition, the Southern California Coastal Water Research Project

(SCCWRP) conducted several hundred trawls within the SCB in the 1970's to 80's. Notable within this effort was the SCCWRP control survey of 1977 that sampled the 60 m isobath from Pt. Conception to the US/Mexico border. More recently, there have been two very large-scale otter trawl surveys conducted as steps towards the development of regional monitoring within the SCB. The first of these was the 1994 Southern California Bight Pilot Project (SCBPP), during which 114 mainland shelf sites were sampled (Allen *et al.* 1998). The sites were randomly allocated across a depth range of 10 to 200 m from Pont Conception to the US/Mexico border. The second regional survey, Bight'98, was conducted July and August of 1998, during the 97/98 El Niño period. Trawls were conducted at 311 sites in depths of 5 to 100 m along the mainland shelf from Pt. Conception to the border, the channel islands and within bays and harbors. A cumulative result of all these surveys is a fairly complete record of the composition of the epibenthic megainvertebrate fauna living on soft bottoms in shelf and upper slope depths within the SCB over the last 30 years. During this period there have been five warm water events classified as El Niños (72/73, 82/83, 86/87, 91/92, 97/98) (Wolter & Timlin 1998). Wicksten (1984) provides a picture of the decapod fauna in the SCB from an earlier period (1900–1930) based upon the collections of the *Anton Dohrn* and other surveys. As in the past 30 years, this was also a period of frequent warm water events (Kiladas and Dias 1989).

The novelty of several heretofore unrecorded decapods in trawl catches in this region during the recent El Niño is accentuated when viewed in the light of the intensity of sampling over the past 3 decades and several El Niños. The possibility that they previously occurred but were not recognized or were merely noted as unidentified shrimp or crabs must be considered. However, this possibility is lessened by the active effort to assure complete and standardized identifications of invertebrate taken in monitoring programs that began in the Bight in the early 1970's. The biologists conducting regular trawl monitoring in the SCB have been active participants in the SCCWRP Taxonomic Standardization Program (1970's) and, since 1982, its successor the Southern California Association of Marine Invertebrate Taxonomists (SCAMIT). The appearance in trawls of unusual or odd organisms is quickly communicated throughout this community and is unlikely to go unnoticed or unrecorded.

The species reported on here have dispersing larval stages: none release larvae brooded to benthic competence. It is possible, therefore, that at least the shrimp species either entered the SCB as larvae, or emigrated as young or adult individuals along with a northward flowing water mass. With the three crab species emigration is not an option, and they arrived either as pelagic larvae, or possibly as passive rafters on debris or other organisms (Martin and Kuck 1991).

Even long term warming trends eventually end in Southern California waters. While local adults may be able to survive in the cooler waters that follow, successful local reproduction probably ceases. Despite the presence of gravid individuals among some of the caridean shrimp (*i.e., Processa peruviana, Pantomus affinis, Plesionika carinirostris*), it is unlikely that any of these populations are able to replace themselves. With the breakdown of El Niño, these isolated pockets are cut off from their source population and disappear with time (as the locally dense population of *Pantomus affinis* in southern Santa Monica Bay apparently has). However, the high frequency of warm water years since 1980 may have allowed these species to gradually extend their range along the Mexican coast northward of their previous known northern limits, placing them within reach of the SCB. If so, we may find these species re-appearing in our catches when oceanographic conditions favor incursion to the north.

Acknowledgments

The authors thank Dr. Michel Hendrickx (Estación Mazatlán, ICML) who examined and confirmed the identity of the pandalid specimens reported upon here, Dr. Mary Wicksten (TAMU) for identifying the processid, Mr. Todd Zimmerman (NHMLAC) for identifications of the palicids, and Mr. Ken Kurtis for permission to use his photograph of *Sicyonia penicillata.* The authors also thank Mr. Atsuhiro Kubo, who produced the drawings of *Plesionika carinirostris* and *Palicus cortezi.* Ronald Velarde, Dean Pasko (CSDMWWD) and Christina Thomas (OCSD) generously provided material and collection information for the records attributed to their agencies. The manuscript benefited from comments received from two anonymous reviewers. This is contribution 14 of SCAMIT.

Literature Cited

Allen, M. J., S. I. Moore, K. C. Schiff, A. B. Weisberg, D. Diener, J. K. Stull, A. Groce, J. Mubarak, C. L. Tang, and R. Gartman. 1998. Southern California Bight Pilot Project: V. Demersal fishes and megabenthic invertebrates. Southern California Coastal Water Research Project. Westminster, California. 324 pp.

Brandt, A. 1993. Redescription of *Notophryxus clypeatus* Sars, 1885, a parasitic isopod of mysidaceans from the Kolbeinsey Ridge, North of Iceland. Sarsia, 78:123–127.

Briggs, J. C. 1974. Marine Zoogeography. McGraw-Hill Book Co. New York, New York. 475 pp.

Burkenroad, M. D. 1934. Littoral Penaeidea chiefly from the Bingham Oceanographic Collection with a revision of *Penaeopsis* and descriptions of two new genera and eleven new American species. Bull. Bingham Oceanographic Collection, 4:1–109.

Burkenroad, M. D. 1938. The Templeton Crocker Expedition. XIII. Penaeidae from the region of Lower California and Clarion Island, with descriptions of four new species. Zoologica, 23:55–91.

Chace, F. A. Jr. 1937. The Templeton Crocker Expedition. VII. Caridean decapod Crustacea from the Gulf of California and the West Coast of Lower California. Zoologica, 22:109–138.

Crane, J. 1937. The Templeton Crocker Expedition. III. Brachygnathous Crabs from the Gulf of California and the West Coast of Lower California. Zoologica, 22:47–78.

Engle, J. and D. Richards. 2001. New and unusual invertebrates discovered at the California Channel Islands during the 1997-1998 El Niño. Bull. So. Cal. Acad. Sci., 100:186–198.

Garth, J. S. 1946. Littoral Brachyuran Fauna of the Galapagos Archipelago. Allan Hancock Pac. Exped., 5:341–600.

Hendrickx, M. E. 1984. The species of *Sicyonia* H. Milne Edwards (Crustacea: Penaeoidea) of the Gulf of California, Mexico, with a key for their identification and a note on their zoogeography. Rev. Biol. Trop., 32:279–298.

Hendrickx, M. E. 1990. The stomatopod and decapod crustaceans collected during the GUAYTEC II Cruise in the Central Gulf of California, Mexico, with the description of a new species of *Plesionika* Bate (Caridea: Pandalidae). Rev. Biol. Trop., 38:35–53.

Hendrickx, M. E. 1992. Distribution and Zoogeographic Affinities of Decapod Crustaceans of the Gulf of California, Mexico. Proc. San Diego Soc. Nat Hist., 20:1–12.

Hendrickx, M. E. 1994. Catalogo de Crustaceos Decapodos y Estomatopodos, Colección de Referencia Estación Mazatlán, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad y Instituto de Ciencias del Mar y Limnologia, Universidad Nacional Autónoma de México. 134 pp.

Hendrickx, M. E. 1995. Camarones. Pp. 417–537 *in* Guia FAO para la identificación de especies para los fines de la pesca. Pacifico centro-Oriental. Vol. 1. Plantas e Invertebrados. (W. Fischer, F.

Krupp, W. Schneider, C. Sommer, K. E. Carpenter y V. H. Niem, eds.) F.A.O. Roma, Italia. 646 pp.

Hendrickx, M. E. 1996. Los Camerones Penaeoidea Bentonicos (Crustacea: Decapoda: Dendrobranchiata) del Pacifico Mexicano. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad y Instituto de Ciencias del Mar y Limnologia, Universidad Nacional Autónoma de México. 147 pp.

Hendrickx, M. E. 1999. Los Cangrejos Braquiuros (Crustacea: Brachyura: Majoidea y Parthenopoidea) del Pacifico Mexicano. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad y Instituto de Ciencias del Mar y Limnologia, Universidad Nacional Autónoma de México. 274 pp.

Hendrickx, M. E., and F. D. Estrada Navarrete. 1996. Los Camerones Pelágicos (Crustacea: Decapoda: Dendrobranchiata y Caridea) del Pacifico Mexicano. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad y Instituto de Ciencias del Mar y Limnologia, Universidad Nacional Autónoma de México. 157 pp.

Hendrickx, M. E., and J. Salgado Barragán. 1997. Capitulo 3. Crustaceos Estomatopodos (Crustacea: Hoplocarida: Stomatopoda) y Decapodos (Crustacea: Decapoda). Pp. 51–90 *in* Tercer Catálog de la Colección de Referencia de Invertebrados. (Hendrickx, M. E., M. C. Espinoza Pérez, J. Salgado Barragán y M. N. Méndez Ubach, eds.) Estación Mazatlán, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad Instituto de Ciencias del Mar y Limnologia, Universidad Nacional Autónoma de México. 90 pp.

Hendrickx, M. E., and M. K. Wicksten. 1989. Los Pandalidae (Crustacea: Caridea) del Pacifico Mexicano, con clave para su identificación. Caldasia, 16:71–86.

Hickey, B. M. 1993. Physical Oceanography. Chapter 2. Pp. 9–70 *in* Ecology of the Southern California Bight, a Synthesis and Interpretation. (M. D. Dailey., D. J. Reish, J. W. Anderson, eds.). Univ. California Press, Berkeley, California. 926 pp.

Kiladis, G. N., and H. F. Diaz. 1989. Global climatic anomalies associated with extremes in the Southern Oscillation. J. Climate, 2:1069–1090.

Koehler, R. 1911. Isopodes nouveaux de la famille des Dajidés provenant des campagnes de la "Princesse-Alice". Bull. Inst. Oceanogr., Monaco, 196:17–34.

Lea, R. N., and F. McAlary. 1994. Occurrence of the Swallow Damselfish, *Azurina hirundo,* from Islands off Southern California. Bull. So. Cal. Acad. Sci., 93:42–44.

Lockington, W. N. 1879. Notes on Pacific coast Crustacea. Bull. Essex Inst., 10:159–165.

Love, M. S., J. E. Cassele, and K. Herbinson. 1998. Declines in nearshore rockfish recruitment and populations in the southern California Bight as measured by impingement rates in coastal electrical power generating stations. Fishery Bulletin, 96:492–501.

Martin, J. W., and H. G. Kuck. 1991. Faunal Associates of an Undescribed Species of *Chrysaora* (Cnidaria, Scyphozoa) in the Southern California Bight, with Notes on Unusual Occurences of Other warm Water Species in the Area. Bull. So. Cal. Acad. Sci., 90:89–101.

Martin, J. W., and R. G. Velarde. 1997. First record of the crab *Pilumnoides rotundus* Garth (Crustacea, Decapoda, Brachyura, Xanthidae sensu lato) from off southern California. Bull. So. Cal. Acad. Sci., 96:105–111.

McGowan, J. A., D. R. Cayan, L. M. Dorman. 1998. Climate-Ocean Variability and Ecosystem Response in the Northeast Pacific. Science, 281:210–217.

Mearns, A. J. 1988. The "odd fish": Unusual occurrences of marine life as indicators of changing ocean conditions. Pp. 137–176 *in* Marine Organisms as Indicators. (D. F. Soule and G. S. Kleppel, eds.) Springer-Verlag. New York, New York. 342 pp.

Méndez, M. 1981. Claves de identification y distribucion de los langostinos y camarones (Crustacea: Decapoda) del mar y rios de la costa del Perú. Boletin del Instituto de Mar Perú-Callao, 5:1–170.

Newman, W. A. 1979. California Transition Zone: significance of short-range endemics. Pp. 399–416 *in* Historical Biogeography, Plate Tectonics, and the changing environment. (Gray, J. & A. J. Boncot, eds.). Oregon State University Press, Portland, Oregon. 500 pp.

Pérez Farfante, I. 1985. The rock shrimp genus *Sicyonia* (Crustacea: Decapoda: Penaeoidea) in the Eastern Pacific. Fishery Bulletin, 83:1–79.

Radovich, J. 1961. Relationship of some marine organisms of the northeast Pacific to water temperature, particularly during 1957 through 1959. Cal. Dep. Fish and Game Bull., 112:1–62.

Rathbun, M. J. 1898. The Brachyura collected by the U.S. Fish Commission Steamer "Albatross" on the Voyage from Norfolk, Virginia, to San Francisco, California, 1887–1888. Proc. U. S. Nat. Mus., 21:567–616.

Rathbun, M. J. 1918. The Grapsoid Crabs of America. Bull U. S. Nat. Mus., 97:1–461.

Smith, S. I. 1871. List of the Crustacea collected by J. A. McNeil in Central America. Report of the Peabody Acad. Sci. for 1869 and 1870:87–98.

Squires, H. J., and J. H. Barragán. 1976. A new species of *Plesionika* (Crustacea, Decapoda, Pandalidae) from the Pacific coast of Colombia. Pac. Sci., 30:113–117.

Stephens, J. S., J. E. Hose and M. S. Love. 1988. Fish assemblages as indicators of environmental change in nearshore environments. Pp. 91–105 *in* Marine Organisms as Indicators. (D. F. Soule and G. S. Kleppel, eds.). Springer-Verlag, New York, New York. 342 pp.

Wicksten, M. K. 1983. A monograph on the shallow water caridean shrimps of the Gulf of California, Mexico. Allan Hancock Monogr. Mar. Bio., 13:1–59.

Wicksten, M. K. 1984. Early Twentieth Century records of marine decapod crustaceans from Los Angeles and Orange Counties, California. Bull. So. Calif. Acad. Sci., 83:12–42.

Wicksten, M. K., and M. E. Hendrickx. 1992. Checklist of penaeoid and caridean shrimps (Decapoda: Penaeoidea, Caridaea) from the Eastern Tropical Pacific. Proc. San Diego Soc. of Nat. Hist., 9: 1–11.

Wolter, K., and M. S. Timlin. 1998. Measuring the strength of ENSO—how does 1997/98 rank? Weather 53:315–324.

Word, J. Q., and D. K. Charwat. 1976. Invertebrates of Southern California Coastal Waters. II. Natantia. Southern California Coastal Water Research Project, El Segundo, California. 238 pp.

Accepted for publication 21 December 2000.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 212–237

Shifts in Fish and Invertebrate Assemblages of Two Southern California Estuaries during the 1997–98 El Niño

Gregory D. Williams,[1] Janelle M. West, and Joy B. Zedler[2]

Pacific Estuarine Research Laboratory,
San Diego State University, San Diego, CA 92182-1870

Abstract.—Estuarine fish and invertebrate assemblages at Tijuana Estuary and Los Peñasquitos Lagoon exhibited changes coincident with the 1997–1998 El Niño event. Three fishes [*Albula* sp. (bonefish), *Ctenogobius sagittula* (longtail goby) and *Acanthogobius flavimanus* (yellowfin goby)] and three invertebrate species [*Callinectes arcuatus* (arched swimming crab), *Penaeus californiensis* (Mexican brown shrimp), and *Petricola hertzana* (bivalve)] were new to estuary monitoring records. In addition, three historically common species exhibited substantial changes in abundance and/or size frequency: *Mugil spp.* (mullet *spp.*), *Grandidierella japonica* (amphipod), and *Tagelus californiensis* (jackknife clam). Likely mechanisms for the observed patterns include modified ocean currents, altered larval supplies, increased rainfall, and flooding disturbance. Long-term biological monitoring programs (12-yr) provided valuable baseline data for quantifying these changes and recording faunal patterns over interannual-decadal time scales.

Introduction

El Niño events are short-term cycles in the ocean-atmosphere system with a mean recurrence interval of 3–8 years (Haston and Michaelsen 1994). In the coastal waters of the Californias, El Niño is characterized by increases in sea-surface temperature and sea level. Most El Niño events also produce abnormally high rainfall and streamflows in southern California (Schonher and Nicholson 1989; Kahya and Dracup 1994). Particularly strong historical El Niño events have occurred in 1926–27; 1957–58, 1982–83, 1991–92, and 1997–98 (Hubbs and Shultz 1929; Simpson 1984; Squire 1987; Lynn et al. 1998). The 1997–1998 El Niño was one of the strongest of this century (Hayward et al. 1999).

In California, the biological effects of El Niño conditions have been documented in many marine habitats. Offshore, these effects include the migration of subtropical or tropical fishes into more northern latitudes (Hubbs and Schultz 1929; Walford 1931; Hubbs 1948; Ketchen 1956; Radovich 1961; Cowen 1985; Squire 1987; Karpov et al. 1995). Enhanced development of a northerly coastal countercurrent (the Davidson current) during El Niño years also results in the northward movement of more southerly pelagic invertebrates (e.g., *Pleuroncodes planipes*; Squire 1987) and fish larvae (e.g., *Semicossyphus pulcher*; Cowen 1985). In nearshore waters, growth and canopy cover of giant kelp (*Macrocystis pyrifera*) declines, with cascading effects on the associated kelp forest community (Dean and Jacobsen 1986; Tegner and Dayton 1987; Dayton et al. 1998). Abundance and nesting success of some seabirds also plummets in El Niño years, presumably due to modification of the nearshore food web (Massey et al. 1992; Veit et al. 1996).

---

[1] Current address: Battelle Marine Sciences Lab, 1529 W. Seqium Bay Road, Sequim, WA 98382.
[2] Current address: University of Wisconsin, Botany Dept., 430 Lincoln Drive, Madison, WI 53706.

Few long-term studies have documented El Niño-related effects on estuarine biota in southern California. Estuarine ecosystems are characterized by substantial variability due to their landscape position at the land-ocean interface, where they are influenced both by their terrestrial watersheds and the tidal marine environment. During El Niño years, high rainfall and streamflows in coastal watersheds can result in rapid flooding, strong freshwater pulses, and substantial sediment deposition in southern California's estuaries and lagoons (Onuf and Quammen 1983). El Niño-related sea level increases and sea storms can lead to dune overwash (Nordby and Zedler 1991) and enhanced inundation of the tidal marsh surface. Together with ocean temperature anomalies and altered current patterns, El Niño-induced natural disturbances may result in a cascade of changes to shallow water estuarine systems. Biotic effects may include a reduction in the diversity and abundance of benthic invertebrate and fish communities (Onuf and Quammen 1983; Nordby and Zedler 1991), invasion by exotic and disturbance-colonizing species, and altered patterns of larval recruitment (e.g., Cowen 1985).

The objectives of our study were to identify trends and anomalies in fish and invertebrate populations from two estuaries in San Diego County during the 1997–98 El Niño. Specifically, we used a 12-year monitoring database to identify the appearance and persistence of new species in these systems coincident with the 1997–98 El Niño, while documenting shifts in historical assemblage composition and size frequency.

Materials and Methods

Study Sites

The Pacific Estuarine Research Laboratory (PERL) at San Diego State University has maintained biological monitoring programs at both Tijuana Estuary (TE) and Los Peñasquitos Lagoon (LPL) since the mid-1980's, enabling comparative ecological research on these unique ecosystems (Nordby and Zedler 1991; Desmond et al. in review). Tijuana Estuary (32°34′N, 117°07′W) is located on the U.S.-Mexico border, at the terminus of the Tijuana River's 4403 km^2 watershed (Fig. 1). At approximately 1024 ha, it comprises one of the largest remaining, intact estuarine habitats of its kind in southern California. It is one of 22 NOAA-designated National Estuarine Research Reserves (NERRs) in the nation (Zedler et al. 1992). TE is strongly influenced by marine conditions and has historically remained open to tidal flushing, with a few exceptions (Zedler et al. 1992). Rapid development of the watershed and floodplain has contributed to the severity of episodic flooding and sedimentation events, often accompanied by chronic sewage flows (Marcus 1989). The sampling program for the NERR was initiated in 1986 to monitor TE's water parameters, soil conditions, and plant, invertebrate, and fish assemblages (Desmond et al. 1999).

Los Peñasquitos Lagoon (32° 56′ N, 117° 15′ W) is a relatively small coastal estuary (252 ha) in northern San Diego County, situated at the outlet of the 420 km^2 Peñasquitos watershed (Fig. 1). The lagoon-marsh complex is protected under its designation as a Natural Preserve, and constitutes the northern portion of Tor-

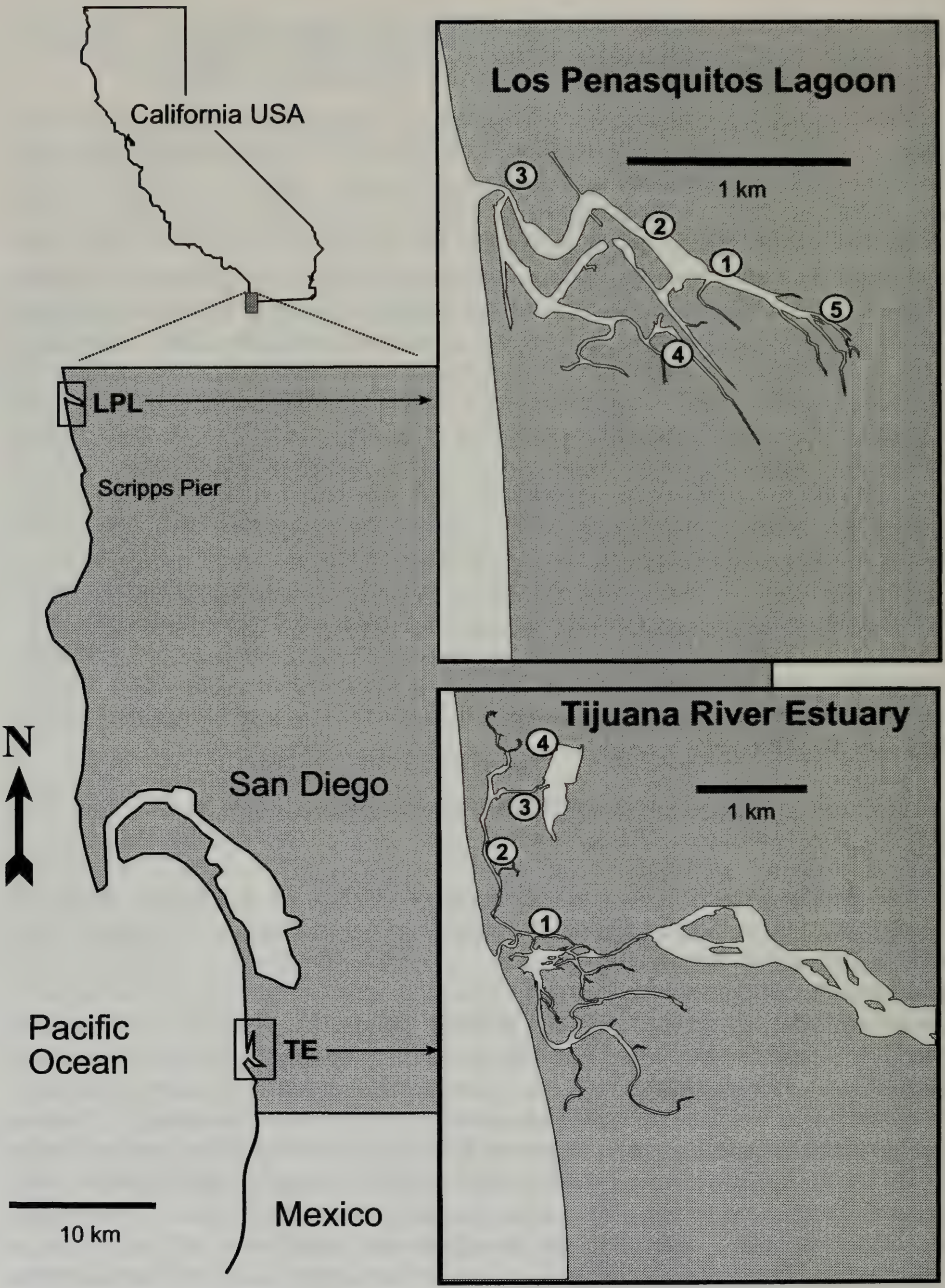

California USA
Los Penasquitos Lagoon
1 km
③
②
①
⑤
④
LPL
Scripps Pier
N
San Diego
Tijuana River Estuary
④
③
②
①
1 km
Pacific Ocean
TE
Mexico
10 km

Fig. 1. San Diego coastal region, with insets of estuarine study sites: Tijuana Estuary (TE; 32° 34′ N, 117° 07′ W) and Los Peñasquitos Lagoon (LPL; 32° 56′ N, 117° 15′ W). Estuarine sampling locations are numbered on inset maps.

rey Pines State Reserve under the jurisdiction of California State Parks. Drainages flowing into LPL include Carroll, Los Peñasquitos, and Carmel Valley Creeks, which were historically perennial streams. LPL closes to tidal flushing on an annual basis, a process more recently augmented by hydrologic modifications (including a major reduction in the tidal prism) associated with construction of a railroad through the lagoon (in 1925), a highway across its mouth (in 1933), and sedimentation from human impacts in the watershed. During closed-mouth conditions, waters become vertically stratified, leading to anoxic conditions and fish kills; since 1986 the management approach to these problems has been to reopen the mouth manually, which enhances tidal mixing and flushing (LPL Foundation and State Coastal Conservancy 1985, Zedler 1996; Williams et al. 1999b). Sampling in Los Peñasquitos Lagoon began in 1986 to monitor water parameters, soil conditions, and plant, invertebrate, and fish assemblages (Williams et al. 1999a).

Physicochemical Conditions

Monthly summaries of rainfall data were obtained from the National Weather Service at Lindbergh Field, San Diego (http://nimbo.wrh.noaa.gov/sandiego-/nws.html). Total monthly streamflows of the Tijuana River at the Nestor gauge were obtained from the International Boundary and Water Commission (IBWC) (http://www.ibwc.state.gov/). Intensive water monitoring was conducted at Oneonta Slough, near Seacoast Drive in the north arm of TE, using an automated YSI 6000 upg datalogger which has been operated and maintained continuously since 1996. This unit samples 6 parameters, including salinity and temperature (°C), at 30-minute intervals, 24 hours a day, with sensors located 10 cm off the bottom of the channel.

Biotic Responses

Identical methods were used to sample invertebrate and fish assemblages at TE and LPL (see below), although sample number and frequency differed. The database at TE includes quantitative estimates (species composition, density, and size-frequency) of fishes and invertebrates collected from three stations (TE#1–3) in the north arm of the estuary (Fig. 1) on a quarterly basis (spring = March, summer = June/July, fall = September, and winter = December/January) from 1986–1999. An additional station in a restoration site (TE#4) was added during 1997–99. At LPL, fishes and invertebrates were initially collected from three stations (LP#1–3; Fig. 1) on a quarterly basis. Sampling frequency at LPL decreased to summer and winter for fishes in 1990, and for invertebrates in 1995, while two additional sampling stations (LP#4 and #5) were added in the upper lagoon in 1995.

Two sets of benthic invertebrate samples were collected at low tide from each station. A first set of nine shallow cores was collected by removing the top 5 cm of sediment with a cylindrical "clam gun" (45 cm length; 15 cm diameter; 176 cm^2 area). The nine cores were combined in groups of three, yielding three replicate samples (0.053 m^2 ea.) from each station. Samples were seived through a 1-mm screen in the field. Easily identifiable animals were counted and released, while all others were preserved in 95% EtOH for later identification; samples were soaked in a rose bengal solution prior to sorting. A second set of "deep" cores was collected by pushing the same "clam gun" 20 cm into the sediment to

Table 1. Number of fish collected at three Tijuana Estuary sampling stations (see Fig. 1 for locations), 1986–1999. * indicate species discussed in this paper.

Family	Species	Common name	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
ALBULIDAE	*Albula* spp.	Bonefish*													9	
ATHERINOPSIDAE	*Atherinops affinis*	Topsmelt	1651	7	2611	3862	489	91	3762	11213	514	857	2838	2445	2949	11967
BLENNIIDAE	*Hypsoblennius gentilis*	Bay blenny			4		1				1		1	2		2
	Hypsoblennius gilberti	Rockpool blenny	1													
	Hypsoblennius jenkinsi	Mussel blenny	1	1												
BOTHIDAE	*Paralichthys californicus*	California halibut	114	65	99	64	93	2	8	3	7	84	66	3	12	13
CARCHARHINIDAE	*Mustelus californicus*	Gray smoothhound								2					1	
COTTIDAE	*Artedius* spp.	Unid. sculpin	2				43									
	Leptocottus armatus	Staghorn sculpin	298	151	671	411	3	8		4	31	51	732	421	14	736
ENGRAULIDAE	*Anchoa compressa*	Deepbody anchovy	2	6			2		98		3	1	14	5		
	Anchoa delicatissima	Slough anchovy					9									
	Engraulis mordax	Northern anchovy														
FUNDULIDAE	*Fundulus parvipinnis*	California killifish	79	937	641	76	234	567	572	1613	4937	548	1734	3566	264	21
GIRELLIDAE	*Girella nigricans*	Opaleye	8	1	1	5			1	1	6					
GOBIIDAE	*Acanthogobius flavimanus*	Yellowfin goby*					1								129	1
	Clevelandia ios	Arrow goby	7617	2222	3795	17124	8482	5515	442	161	5856	564	1533	3775	398	556
	Ctenogobius sagittula	Longtail goby*													65	1
	Gillichthys mirabilis	Longjaw mudsucker	39		233	4	8	6	11	32	3	889	37	28	123	17
	Ilypnus gilberti	Cheekspot goby	45	5	2	219	38	2		2	8	32	77	8	12	71
	Lepidogobius lepidus	Bay goby					2	65								
	Quietula y-cauda	Shadow goby	3				96									
MUGILIDAE	*Mugil* spp.	Mullet*	3	2			29		24		4	9	17	356	185	268
PLEURONECTIDAE	*Hypsopsetta guttulata*	Diamond turbot	13	33	36	3	34	2	5	2	53	24	67	44	12	45
	Pleuronichthys ritteri	Spotted turbot	3	1												

Table 1. Continued.

Family	Species	Common name	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
	Pleuronichthys coenosus	C–O turbot									1			4		1
POECILIDAE	*Gambusia affinis*	Mosquitofish				2										
RHINOBATIDAE	*Rhinobatos productus*	Shovelnose guitarfish	2													
SCIAENIDAE	*Seriphus politus*	Queenfish	1													
SERRANIDAE	*Paralabrax clathratus*	Kelp bass		1	8						1					
	Paralabrax maculatofasciatus	Spotted sand bass														1
	Paralabrax nebulifer	Barred sand bass											1	3		
SYNGNATHIDAE	*Syngnathus leptorhynchus*	Bay pipefish	6	1	5					1		1	1	3		4
TOTAL FISH COLLECTED			9888	3433	8106	21770	9564	6258	4923	13034	11425	3060	7118	10663	4173	13704

estimate the abundance of large, deep-dwelling invertebrates (e.g., bivalves, burrowing shrimp). Nine cores, pooled using the same methods as in the shallow series, were taken at each station. Samples were seived through a 3-mm screen in the field. Easily identifiable animals were counted and released, others were preserved as above for later identification. Field observations, including those made of specimens captured during fish seining (see below), provided additional data on large and/or mobile taxa not usually sampled with the cores. Because invertebrate monitoring focused on benthic invertebrates, our protocol for surface macroinvertebrates was to note the presence of the more mobile taxa (e.g. *Pachygrapsus crassipes* on banks of channels). When unusual species appeared, their presence was noted and, time permitting, density and/or size data were gathered.

Fishes and mobile surface macroinvertebrates (e.g., decapod crustaceans) were sampled from each station during the slack period of a low neap tide using two blocking nets and one 15-m bag seine with 3-mm square delta mesh. At each study site a linear distance (~9 to 12 m) was measured parallel to the channel and two blocking nets were deployed to confine all fishes within this area. The bag seine was then swept between the two blocking nets and across the channel to the opposite bank (defining 1 pass). Passes were repeated until the number of fish captured per pass was less than 5% of the total catch. The species composition and number of fishes collected was recorded separately for each pass. Subsamples of at least 25 individuals per fish species were measured and then released outside the blocking nets. Individuals that were unique or difficult to identify were preserved as voucher specimens.

Historical data (i.e., Tables 1–3) was used to identify groups of fish and invertebrate species that exhibited atypical abundance trends coinciding with the strong 1997–98 El Niño event. Although another fairly strong El Niño event (1991–92) has occurred during our long-term monitoring program, our data indicated minimal responses to this event among the biotic communities of TE and LPL (Tables 1–3). However, because the 1997–98 event had a striking effect on these two systems, we focused on 1997–98 data from both LPL and TE, identifying species new to the sampling record and reporting long-term trends in abundance (density) and size-structure.

Results and Discussion

Physicochemical Conditions

Monthly multivariate El Niño indices indicate that strong El Niño conditions extended from April 1997 through July 1998 along the southern California coast (Hayward et al. 1999). During this time, sea-surface temperatures were anomalously warm, averaging from 2–4 °C above long-term means (Lynn et al. 1998). El Niño conditions also produced a substantial increase in mean water levels during this time, with a maximum anomaly of +0.2 m at the Scripps Pier (La Jolla, CA) in November 1997 (Lynn et al. 1998).

Precipitation during the 1997–98 water year (7/1/97–6/30/98) was over 45 cm, which exceeded the long-term average of 25.4 cm yr^{-1} recorded at Lindbergh Field, San Diego (Fig. 2). An exceptional peak in February 1998 rainfall (19.4 cm) was almost equal to the long-term annual mean. Rain events were accompanied by elevated river flows. At the U.S.-Mexico border in April 1998, Tijuana

Table 2. Number of fish collected at five Los Peñasquitos Lagoon sampling stations (see Fig. 1 for locations), 1986–1999. * indicate species discussed in this paper.

Family	Species	Common name	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
ATHERINOPSIDAE	*Atherinops affinis*	Topsmelt	1668	416	1456	6479		1262	222	181	2327	842	784	5176	257	963
BOTHIDAE	*Paralichthys californicus*	California halibut	6	4	7	1		1		2	5	1	15	3	1	3
CENTRARCHIDAE	*Lepomis cyanellus*	Green sunfish														1
	Micropterus sp.	Unid. bass													1	
COTTIDAE	*Leptocottus armatus*	Staghorn sculpin	94	23	11	376	3	1	14	15	4	67	14	16		
EMBIOTOCIDAE	*Cymatogaster aggregatta*	Shiner surfperch										1				
ENGRAULIDAE	*Anchoa compressa*	Deepbody anchovy	236	11	56	21				13	119	44	5	139	15	21
	Anchoa delicatissima	Northern anchovy						3	1							
FUNDULIDAE	*Fundulus parvipinnis*	California killifish	26	124	61	237	2	11	137	3	149	45	66	42	13	22
GIRELLIDAE	*Girella nigricans*	Opaleye	1						1		2			1		
GOBIIDAE	*Acanthogobius flavimanus*	Yellowfin goby*				6				3	2				32	25
	Clevelandia ios	Arrow goby	17	55	57	236	23	18	1	53	12	9	44	27	66	127
	Ctenogobius sagittula	Longtail goby*													4	
	Gillichthys mirabilis	Longjaw mudsucker	111	298	536	295	2	99	18	7	2	13	21	48	32	4
	Ilypnus gilberti	Cheekspot goby			18	34							3	2	63	2
	Lepidogobius lepidus	Bay goby		9				11								
	Quietula y-cauda	Shadow goby						4			137		838	1671	256	871
MUGILIDAE	*Mugil* spp.	Mullet*			3						5	6	1	2	163	128
PLEURONECTIDAE	*Hypsopsetta guttulata*	Diamond turbot	1	3	11				5		16		11	15	13	14
	Pleuronichthys ritteri	Spotted turbot						1								
POECILIIDAE	*Gambusia affinis*	Mosquitofish	6	7	928	394				1			4	41	3	33
SCIAENIDAE	*Menticirrhus undulatus*	CA corbina													2	
	Umbrina roncador	Yellowfin croaker										1				
SERRANIDAE	*Paralabrax clathratus*	Kelp bass									2					
	Paralabrax maculatofasciatus	Spotted sand bass									3					
	Paralabrax nebulifer	Barred sand bass						1								
SYNGNATHIDAE	*Syngnathus leptorhynchus*	Bay pipefish	13		2			1		8	16		23	1	6	26
TOTAL FISH COLLECTED			2179	950	3659	10779	30	1413	489	1251	2891	1029	1829	7184	1071	2636

Table 3. Decapods observed at Tijuana Estuary and Los Peñasquitos Lagoon, 1991–1999. * indicate species discussed in this paper.

		Tijuana Estuary									Los Peñasquitos Lagoon								
		1991	1992	1993	1994	1995	1996	1997	1998	1999	1991	1992	1993	1994	1995	1996	1997	1998	1999
CALLIANASSIDAE	*Neotrypaea californiensis*	X	X		X	X	X	X		X				X	X	X			
CANCRIDAE	*Cancer* sp.								X										
CRANGONIDAE	*Crangon* sp.				X										X				
GRAPSIDAE	*Hemigrapsus oregonensis*	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	Pachygrapsus crassipes	X				X	X	X						X	X	X	X	X	X
HIPPOLYTIDAE	*Hippolyte californiensis*					X		X		X						X	X	X	X
OCYPODIDAE	*Uca crenulata*						X							X	X	X	X	X	
PALEOMONIDAE	*Palaemon macrodactylus*					X		X		X				X	X	X	X	X	X
PAGURIDAE	*Pagurus* sp.				X	X		X											
PENAEIDAE	*Penaeus californiensis**							X	X								X	X	
PORTUNIDAE	*Callinectes arcuatus**								X	X								X	X
	Portunus xantusii							X	X							X	X	X	
UPOGEBIIDAE	*Upogebia pugettenis*			X						X									
XANTHIDAE	*Lophopanopeus bellus*							X		X						X			
	Lophopanopeus frontalis															X			

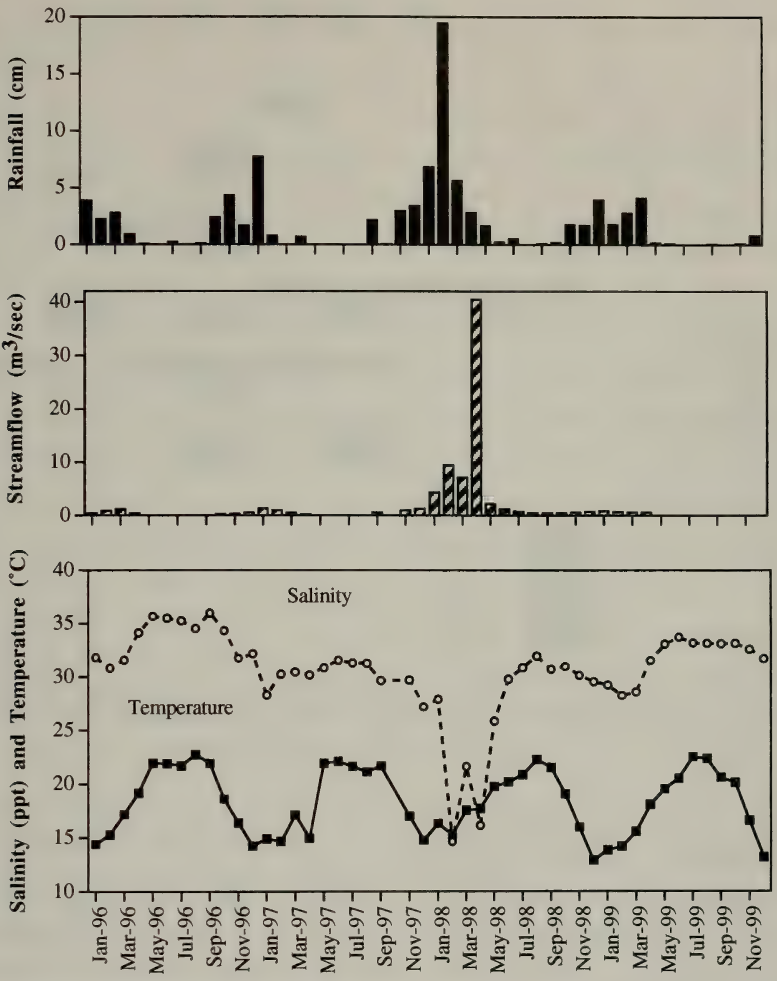


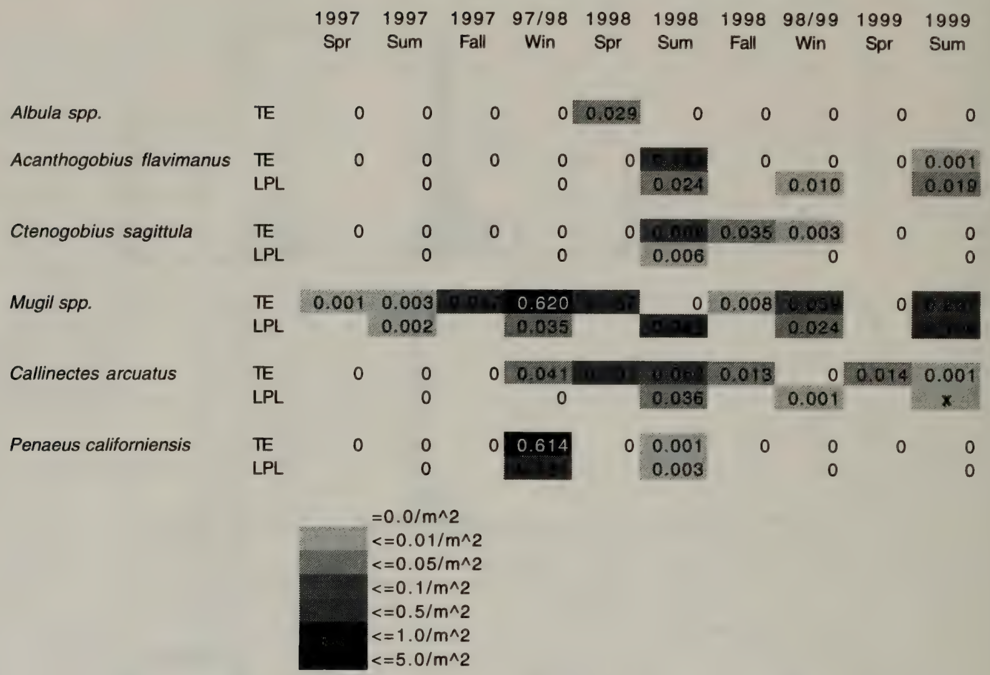
Fig. 2. Total monthly rainfall (cm; top) and mean monthly streamflow (m^3 sec^{-1}; middle) in the Tijuana River. Mean monthly salinity and temperature (ppt, °C; bottom) within Tijuana Estuary, as measured by YSI datalogger at station TE#2. El Niño conditions persisted from approximately April 1997–July 1998.

River flows exceeded 40 m^3 sec^{-1}; mean daily flow rates at this site (since 1962) were 2.31 m^3 sec^{-1}. No river gauges are maintained in the lower watershed of Los Peñasquitos Lagoon.

Exceptional precipitation and river flow-rates also impacted estuarine habitats, where flooding deposited up to 12 cm of sediment over Tijuana Estuary mudflats (Ward 2000). Dramatic declines in mean monthly water salinities at TE#2 during February and April 1998 corresponded with periods of high rainfall and water flows (Fig. 2).

Biotic Responses

Based on differences before and during the 1997–1998 El Niño event, we observed six fish and invertebrate species that were either historically uncommon



		1997 Spr	1997 Sum	1997 Fall	97/98 Win	1998 Spr	1998 Sum	1998 Fall	98/99 Win	1999 Spr	1999 Sum
Albula spp.	TE	0	0	0	0	0.029	0	0	0	0	0
Acanthogobius flavimanus	TE	0	0	0	0	0	[illegible]	0	0	0	0.001
	LPL		0		0		0.024		0.010		0.019
Ctenogobius sagittula	TE	0	0	0	0	0	[illegible]	0.035	0.003	0	0
	LPL		0		0		0.006		0		0
Mugil spp.	TE	0.001	0.003	[illegible]	0.620	[illegible]	0	0.008	0.059	0	[illegible]
	LPL		0.002		0.035		[illegible]		0.024		[illegible]
Callinectes arcuatus	TE	0	0	0	0.041	[illegible]	[illegible]	0.013	0	0.014	0.001
	LPL		0		0		0.036		0.001		x
Penaeus californiensis	TE	0	0	0	0.614	0	0.001	0	0	0	0
	LPL		0		[illegible]		0.003		0		0

=0.0/m^2
<=0.01/m^2
<=0.05/m^2
<=0.1/m^2
<=0.5/m^2
<=1.0/m^2
<=5.0/m^2

Fig. 3. Mean density (per m²) of species collected with the seine (spring 1997 through summer 1999) that exhibited atypical abundance trends during the 1997–98 El Niño event. "X" indicates that individuals were observed in low numbers, but densities were not quantified.

or completely new to the monitoring record. During 1997–98 we also documented shifts in abundance (increase or decrease) and/or size structure of three species that were common in the historical monitoring record. Descriptive analysis of these species trends includes the date of first collection, density and relative abundance, persistence in the estuary, size frequency, and discussion of life history.

New/uncommon species.—Most of the fish and invertebrate species new to the 12-year monitoring record at TE and LPL in 1997–98 were collected as juveniles. Their appearance altered the relative abundance of common species and increased species richness in lagoon assemblages. New invertebrates were first collected in winter 1997–98, while fishes were collected later in the summer or fall of 1998, either due to differential catchability or real differences in larval arrival/availability (Fig. 3). Each species exhibited variable periods of persistence in these estuaries. Although it appears that the abundance of several other species (*Portunus xantusii*—Xantus' swimming crab, *Paralabrax nebulifer*—barred sand bass, *Menticirrhus undulatas*—California corbina, and *Pleuronichthys coenosus*—C-O turbot) may also be correlated with the 1997–98 El Niño event (Tables 1 and 2), we are not considering these as "new/uncommon species" because they are all regularly found in the local sandy nearshore environment.

Albula sp. (bonefish): A total of 11 *Albula spp.* leptocephalus larvae were collected at TE in spring 1998 (Table 1; Fig. 3). While not abundant (mean density < 0.03 m^{-2}; $< 4\%$ relative abundance), *Albula spp.* leptocephali were collected at 3 of 4 sampling stations, indicating wide distribution throughout the estuary. *Albula* leptocephali in the Gulf of California grow to lengths of up to 70 mm standard length (SL) prior to settlement (Pfeiler 1984). Individuals in our collections ranged in size from 38–68 mm total length (TL).

This is the first time this tropical species has been collected at TE since monitoring was initiated in 1986 (Table 1); none have been collected at LPL. No additional *Albula spp.* (larvae, juveniles, or adults) were collected in 1999 or 2000, suggesting that this species did not persist in the estuary either due to outmigration, mortality, or our inability to capture juvenile stages or adults. Unusual recruitment of *Albula spp.* was also observed in 1998 at nearby Mission Bay (Talley 2000) and San Diego Bay (Allen 1998).

Because of current uncertainties regarding the taxonomic identity of bonefish in our region (Pfeiler et al. 1988), we refer to specimens in our collections as *Albula spp.* Bonefish are oviparous and presumably have planktonic eggs; larvae are rare in collections from the California Current region, although they are common and widespread in the Gulf of California (Moser et al. 1993, Charter and Moser 1996). Pfeiler et al. (1988) postulated that *Albula* leptocephali from the Gulf of California have a larval duration of 6–7 months; during winter and spring months the larvae actively move into shallow, lagoon nurseries in the first hours of a nocturnal flood tide, where they metamorphose into juveniles (Pfeiler 1984). *Albula* leptocephali are euryhaline, with a salinity tolerance of 4–52 ppt; they have been reported in both hyper- and hypo-saline lagoon habitats (Pfeiler 1981). Adult bonefish constitute an important recreational fishery in many areas and typically inhabit shallow (<0.5 m) sand and seagrass flats, where they feed on a variety of benthic prey (Mojica et al. 1994, Charter and Moser 1996).

Ctenogobius sagittula (longtail goby): The tropical goby, *Ctenogobius sagittula,* was first sampled at TE and LPL during summer 1998 (Tables 1 and 2). At TE, 65 *C. sagittula* were collected from stations TE#2 and TE#3 in channels of moderate depth (0.25–0.6 m on a low, neap tide), with strong tidal flows and bottoms composed of muddy sand or shell hash. Mean density across all stations was <0.09 m^{-2} (Fig. 3), with *C. sagittula* averaging over 20% of the catch. *Ctenogobius sagittula* persisted in TE for approximately six months, becoming less common in quarterly samples subsequent to summer 1998. Mean densities decreased to 0.035 fish m^{-2} by fall 1998 and <0.01 m^{-2} by winter 1998–99. Mean *C. sagittula* sizes rapidly increased from 55.6 mm during summer 1998 (range: 33–78 mm TL), to 123.6 mm by fall 1998 (range: 98–200 mm TL).

Ctenogobius sagittula was less abundant at LPL. During the June 1998 sampling period, a total of four *C. sagittula* measuring 88–93 mm TL were collected from one station (LP#2), which is located in a warm, shallow side-channel near the lagoon interior (Fig. 1). *Ctenogobius sagittula* made up $<2\%$ of the mean catch across all stations, with mean densities of 0.03 fish m^{-2} (Fig. 3). This is the only LPL record of *C. sagittula*; no individuals were collected in subsequent samples. Specimens from both locations have been archived in the Scripps Institution of Oceanography vertebrate collections (TE—SIO 98-124; LPL—SIO 98-123).

Ctenogobius sagittula is currently considered rare (Miller and Lea 1972) or extirpated (Swift et al. 1993) in southern California. However, the species is common in the Gulf of California and adjacent waters to Panama (Ruiz-Campos and Castro-Aguirre 1999), with disjunctive records in warmer Pacific coastal lagoons of Baja California, Mexico (e.g., San Ignacio lagoon by De La Cruz-Aguero and

Cota-Gomez 1998, San Quintin Bay by Rosales-Casian 1996). *Ctenogobius sagittula* was also observed during spring and summer of 1998 in Mission Bay marshes (Talley 2000).

Acanthogobius flavimanus (yellowfin goby): Another historically rare goby, the nonindigenous *Acanthogobius flavimanus* also appeared during summer 1998 sampling at both TE and LPL (Fig. 3). At TE, *A. flavimanus* was collected at densities of 0.49 m^{-2} at one station (TE#2) in the main channel of the north arm. Averaged across all 3 stations, *A. flavimanus* densities were 0.16 m^{-2} (4.9% of the total catch). All *A. flavimanus* collected at this time were juveniles (<100 mm TL; Baker 1979) with a size range of 28–88 mm TL. This recruitment pulse appeared to be a one-time event at TE; the only *A. flavimanus* specimen observed since then has been a single 38 mm TL individual collected in June 1999. The absence of adults in subsequent TE collections suggests that *A. flavimanus* populations do not persist for long in TE, with recruitment events likely dependent on an influx of larvae supplied from other locations (perhaps San Diego Bay; Williams et al. 1998a).

A recruitment pulse of *Acanthogobius flavimanus* was also observed in summer 1998 at LPL, where their mean density was 0.02 m^{-2} and they averaged 6.4% of the catch across all stations (Fig. 3). Most of these specimens were collected in the mid-lagoon channels of station LP#1 and LP#2, and ranged in size from 58–128 mm TL, considerably larger than those collected at TE two weeks later. However, *A. flavimanus* were prevalent throughout the lagoon, including upper lagoon stations LP#4 and LP#5 where surface salinities were low (3–5 ppt) and generally reflected heavy freshwater inputs (Fig. 1). The summer 1998 cohort of *A. flavimanus* presumably persisted in LPL through the next year, growing into mature individuals (150–220 mm TL) that were later collected both in winter 1998–99 and summer 1999. A new recruitment pulse of juveniles (47–133 mm TL) also came into the lagoon in summer 1999 at densities averaging 0.02 m^{-2} (3.4% of the total catch).

Acanthogobius flavimanus is becoming increasingly common in San Diego County estuaries. Previous studies documented the southern expansion of *A. flavimanus* to San Diego Bay (32°34′N, 117°5′W) in 1989 (Williams et al. 1998a). However, unpublished records show that a single 96-mm individual was previously collected at TE in 1990 under the NERR fish monitoring program (Table 1). *Acanthogobius flavimanus* individuals have been collected episodically at LPL during summer sampling periods in 1989, 1993, and 1994 (Table 2) and during fish kills coinciding with extended mouth closure events (G. Williams, pers. obs.). Tolerant to a wide range of salinities and temperatures, this large (to 290 mm TL), opportunistic carnivore may negatively impact native fish assemblages, especially in disturbed habitats (Baker 1979, Usui 1981). While the extending range and increasing abundance of *A. flavimanus* is apparent, the long-term ramifications of these changes are unclear. However, resource managers should be aware of this species' presence and potential impacts to the ecology of native aquatic communities (Williams et al. 1998a).

Callinectes arcuatus (arched swimming crab): This crab species is typically found in estuarine mud or sand substrates (Garth and Stephenson 1966, Paul 1982a). It was initially collected with the seine at TE in winter 1997–98 (0.041 individuals m^{-2}) and at LPL in summer 1998 (0.036 individuals m^{-2}) (Fig. 3).

Additional specimens were observed at this time in several nearby estuaries, including the San Diego River channel and Sweetwater Marsh on San Diego Bay (G. Williams and J. West, pers. obs.), as well as Mission Bay (Talley 2000). Southern California represents the northern extension of *C. arcuatus*' known geographic range, which continues south to Peru (Williams 1974).

At TE, *C. arcuatus* was most abundant during the main pulse of the El Niño event (winter 1997–98 through summer 1998; Fig. 3). *Callinectes arcuatus* had peak densities of 0.101 individuals m^{-2} during spring 1998, with a mean carapace width (CW) of 61.1 mm (range: 40–119 mm). As *C. arcuatus* densities declined throughout the following year, the population structure shifted to predominantly larger adults. *Callinectes arcuatus* is known to exhibit rapid growth rates of about 8 mm/month, reaching maturity at 80 mm carapace width (CW) (Paul 1982b). By spring 1999, *C. arcuatus* densities had declined substantially (0.014 individuals m^{-2}), while the mean size of collected individuals increased to 123.7 mm CW (range: 105–145 mm). None were collected after summer 1999 (Desmond et al. 2000). At LPL, *C. arcuatus* was most abundant in summer 1998 (0.036 individuals m^{-2}); densities dropped dramatically by winter 1998–99 (0.001 individuals m^{-2}; Fig. 3).

Callinectes arcuatus is considered a euryhaline species tolerant of a wide range of temperatures. In the Gulf of California it occurs in areas with salinities ranging from 1–65 ppt and temperatures from 17.5–34°C (Paul 1982a). In a western Mexico lagoon system, *C. arcuatus* fed primarily on bivalves (particularly *Tagelus affinis*), crabs, and fish, while shrimp and gastropods were consumed in lesser amounts (Paul 1981).

Penaeus californiensis (Mexican brown shrimp): Juvenile *Peneaus californiensis* were collected with the seine at TE and LPL in winter 1997–98 and summer 1998 (Fig. 3). Seine samples were generally made in shallow water ~1 m depth, and all individuals collected were juveniles between 14–37 mm carapace length (CL). There is no previous collecting record of this species at either LPL or TE, although their native range spans the coast from San Francisco Bay to Peru (Dore and Frimodt 1987).

The mean density of *P. californiensis* at TE during winter 1997–98 was 0.614 individuals m^{-2}, yet none were collected the following spring (Fig. 3). LPL densities during winter 1997–98 were lower than at TE (0.131 individuals m^{-2}); LPL was not sampled in spring 1998. By summer 1998, *P. californiensis* densities had declined to < 0.005 individuals m^{-2} at both LPL and TE.

Penaeus californiensis is an important commercial species in Mexico, where it constitutes up to 75% of the Mexican Pacific shrimp catch (Dore and Frimodt 1987; Magallon-Barajas 1987). Newly hatched larvae travel up coastal estuaries into lagoons, where they spend several months growing to a "subadult" stage before returning to sea to mature and spawn (Snyder-Conn and Brusca 1975; McGoodwin 1979). Mature adults, which can reach a maximum size of 210 mm CL, generally occur on muddy bottoms or sandy mud at depths of 25–50 m (Dore and Frimodt 1987). In the Gulf of California, *P. californiensis* abundance naturally peaks during the winter season, and most individuals live only one year (Snyder-Conn and Brusca 1975). The *P. californiensis* fishery in the Gulf of California experiences substantial interannual variation in catch per unit effort, likely due to strong recruitment events, which have been positively correlated with elevated

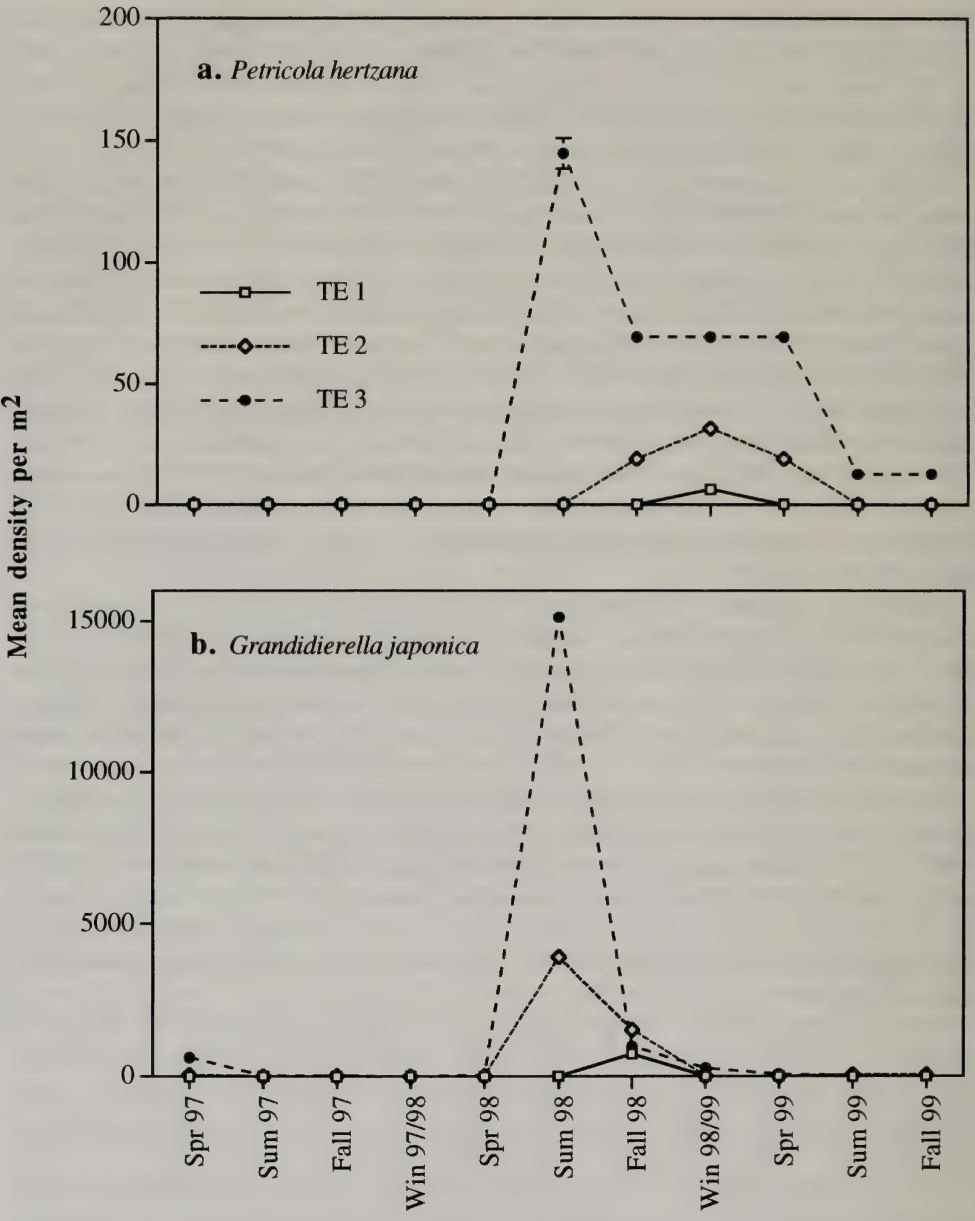


Fig. 4. *Petricola hertzana* (a) and *Grandidierella japonica* (b) densities (± SE) at three Tijuana Estuary sampling stations from spring 97 through fall 1999.

sea temperature anomalies characteristic of El Niño events (Morales-Bojorquez and Lopez-Martinez 1999).

Petricola hertzana: The bivalve *Petricola hertzana* (Petricolidae) was first encountered during summer 1998 in benthic core samples collected at station TE#3, where mean densities reached 145 individuals m^{-2} (Fig. 4a). Since this initial collection date, *P. hertzana* abundance has generally decreased, although the species continues to persist at low densities (~35 individuals m^{-2}) at this site. During fall 1998 *P. hertzana* was also observed at a nearby station, TE#2. The population at this site gradually increased, reaching a peak in winter 1998–99 (45 individuals m^{-2}). No *P. hertzana* individuals have been collected at TE#2 since spring 1999 (Fig. 4a).

Petricola hertzana is known to nestle among algae (Coan 1997), and adults range in size from 6–11 mm shell length (SL; McLean 1969). Individuals collected in our samples ranged from 1–11 mm, indicating the presence of both juveniles and adults. The distribution of *P. hertzana* ranges from Santa Monica Bay to Magdalena Bay, Baja California Sur (Coan 1997). Another *Petricola* species (identified as *P. pholadiformis,* which may in fact be *P. hertzana*) was documented in samples conducted at TE from September 1986 to June 1987 (Duggan 1989).

Historically common species.—Several historically common fish and invertebrate species at TE and LPL exhibited a substantial change (increase or decrease) in abundance during 1997–98, often accompanied by shifts in size-frequencies.

Mugil spp. (mullet): Mullet (*Mugil spp.*) are large, schooling fish with a cosmopolitan distribution that reach maturity at approximately 300 mm TL (2–3 years) (Anderson 1958). Adult *Mugil cephalus* are common and conspicuous in southern California estuaries and they likely dominate fish biomass in these systems; however, they are generally not sampled effectively due to their size and mobility (Allen 1982, Horn and Allen 1985, Williams et al. 1999a, Desmond et al. 1999). Smaller juveniles, which can be more effectively sampled with most gear (e.g., seines), have historically been rare in these collections (Desmond et al. 1999). Low numbers of *Mugil curema* (white mullet) have also been collected in southern California waters, and may easily be confused with *M. cephalus,* especially as juveniles (Lea et al. 1988). We therefore treat mullets as *Mugil* spp. throughout the remainder of the paper, although *M. cephalus* is likely the dominant species. In both winter 1997–98 and spring 1998, *Mugil spp.* juveniles were a major component of catches at TE (22–23% total catch).

Young-of-the-year (YOY) *Mugil spp.* (41–50 mm TL) were first collected in September 1997 throughout TE (3 of 4 stations) at average densities of 0.09 m^{-2} (Fig. 3). Small juveniles 18–43 mm TL continued recruitment through December 1997, when they were collected at all four sampling stations at average densities of 0.63 m^{-2} (17.7% of catch) (Fig. 5). Thereafter, TE mean densities fluctuated considerably but exhibited a general decline, while mean individual size increased. By September 1998 (one year post-recruitment), average *Mugil spp.* size was 165 mm TL; by June 1999, the average size had increased to 265 mm TL (Fig. 5), indicating a growth rate of between 75 and 125 mm per year at TE.

Under the semiannual sampling schedule at LPL, juvenile *Mugil spp.* were first collected in winter 1997/98 at mean densities of 0.035 m^{-2} (Fig. 3; 11.7% of the total catch). Abundance of juvenile *Mugil spp.* peaked the following summer (1998) at 0.32 m^{-2}, when they were collected at all 5 stations and composed 40.9% of the total catch. Mean size at this time was 76 mm TL (Fig. 5). *Mugil spp.* were still abundant at LPL one year later (summer 1999), but by this time average size had increased to 175 mm TL. A comparison of *Mugil spp.* cohort growth rates from LPL and TE suggests that individuals from LPL may grow at a slower pace.

During the spring of 1998, Talley (2000) and Allen (1998) also noted increases

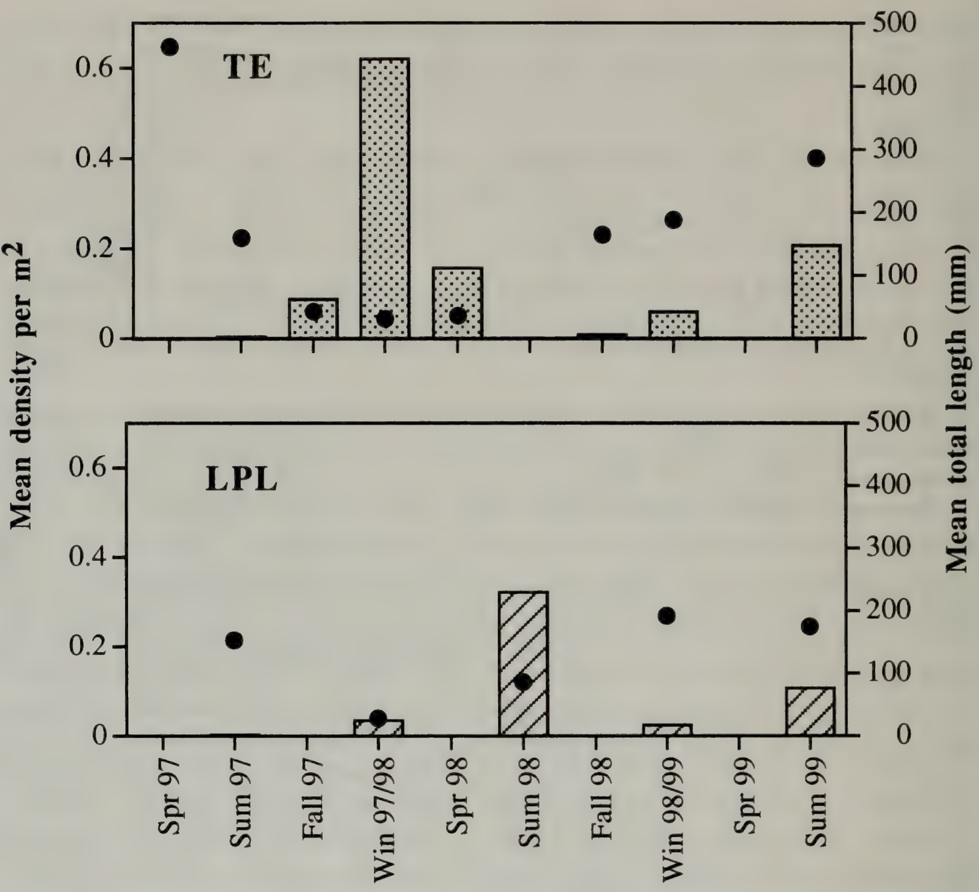


Fig. 5. Columns represent mean density (per m^2) of *Mugil spp.* collected seasonally (spring 1997 to summer 1999) at Tijuana Estuary (TE; top) and Los Peñasquitos Lagoon (LPL; bottom). Black dots indicate the mean total length (mm) of individuals collected.

in the abundance of juvenile *Mugil spp.* from surveys made in Mission Bay and San Diego Bay, respectively. *Mugil spp.* are found in most warm seas, including the Eastern Pacific from the Galapagos Islands to San Francisco Bay. They are oviparous, with planktonic eggs and larvae (Sandknop and Watson 1996). Adult *Mugil spp.* spawn in surface waters offshore and enter bays and estuaries as juveniles or larvae (Anderson 1958), often moving upstream into freshwater rivers where they develop as yearlings (Follett 1960). Small numbers of mugilid larvae have been collected during annual ichthyoplankton surveys (1951–1984) conducted in the California Current region; the highest larval concentrations occur in nearshore stations off central and southern Baja California during the summer and fall (Moser et al. 1993, Sandknop and Watson 1996).

Grandidierella japonica: This exotic corophiid amphipod exhibited a population explosion throughout TE during summer/fall 1998. The highest mean *G. japonica* densities at TE#3 (15,119 individuals m^{-2}) and TE#2 (3904 m^{-2}) were observed in summer 1998, while TE#1 (1113 m^{-2}) peaked in fall 1998 (Fig. 4b). By winter 1998–99, mean *G. japonica* density across all sites (96.4 m^{-2}) had declined substantially, approaching long-term historical densities (mean for 1994–97 = 93.5 m^{-2}). LPL populations of *G. japonica* also experienced an abundance peak during the 1997–98 El Niño event. The mean density across all sites in winter 1997–98 was 643 individuals m^{-2}, three times greater than the long-term average of 203 individuals m^{-2} (Williams et al. 1998b). After this substantial peak in abundance, *G. japonica* densities dropped to levels near the long-term average during the following seasons.

The introduction of *G. japonica* into the United States was first reported in San Francisco Bay, California in 1966 (Chapman and Dorman 1975). It was identified in TE samples in 1994, but may have been present and unidentified in TE prior to this. *Grandidierella japonica* is native to Japan and is typically associated with brackish water and soft sediments, where it inhabits U-shaped tubes. In laboratory studies, *G. japonica* is capable of producing 10–12 generations per year (Greenstein and Tiefenthaler 1997), which could explain the dramatic increase in densities that occurred within a relatively short time period.

Rapidly reproducing, opportunistic species increase in abundance following a disturbance if they can take advantage of expanded resources (McCall 1977; Rhoads et al. 1978; Zajac and Whitlatch 1982). El Niño-related winter storms in 1997–1998 caused heavy sedimentation in Tijuana Estuary (Ward 2000), which may have smothered other invertebrates and decreased competition for resources. *G. japonica* densities in Yaquina Bay, Oregon also increased dramatically following a flood event (B. Boese, pers. comm.).

Tagelus californiensis (jacknife clam): This long-time dominant of the invertebrate community at both TE and LPL (Emmett et al. 1991; Desmond et al. 1999; Williams et al. 1999a), exhibited substantial declines at TE during the 1997–98 El Niño event. In spring 1997, the *T. californiensis* population at TE#2 was composed of individuals ranging in size from 28–70 mm shell length (SL) at a mean density of 145 individuals m^{-2} (Fig. 6). Densities gradually declined during summer and fall 1997 (57 and 13 m^{-2}, respectively). No live *T. californianus* individuals were collected (although many empty shells were found) during winter 1997–98 or spring 1998, which coincided with rain and flooding in the estuary. Summer 1998 collections were marked by an influx of new recruits ranging in size from 7–15 mm SL at densities of 138 m^{-2} (Fig. 6). Although *T. californianus* densities decreased in the following months (94 m^{-2} in fall 1998, 57 m^{-2} in winter 1998–99), summer 1999 collections had high densities (270 m^{-2}). However, even by the summer of 1999, the population at TE#2 was still composed entirely of juveniles (10–56 mm SL).

Tagelus californiensis has a wide geographic distribution, ranging from Cape San Lucas, Baja California, Mexico to Cape Blanco, Oregon, but it is most abundant from TE to Morro Bay, California (Emmett et al. 1991). *Tagelus californiensis* occupies a permanent burrow where it feeds on phytoplankton and other suspended particles (Morris et al. 1980). Sexual maturity is reached between 60–120 mm shell length (Merino 1981). Peak spawning of *T. californianus* occurs in spring, with some limited spawning continuing year-round (Emmett et al. 1991).

Summary and Conclusions

Observed changes in the fish and invertebrate assemblages at TE and LPL during 1997–98 were likely related to El Niño-driven ocean anomalies (altered

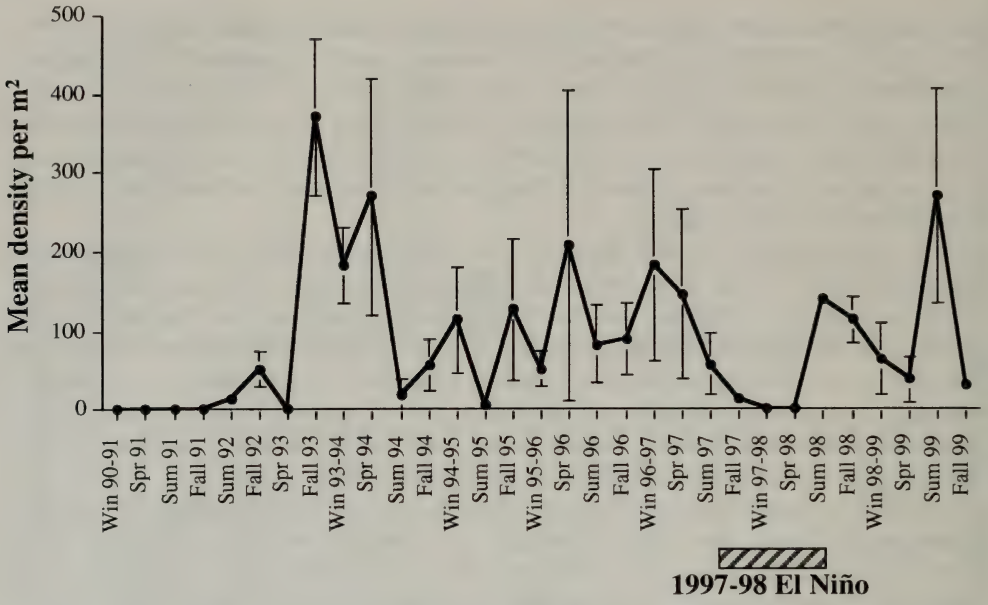


Fig. 6. Mean density of *Tagelus californianus* (jacknife clam) collected seasonally (winter 1990–fall 1999) in 20-cm-deep cores at Tijuana Estuary sampling station TE#2. Error bars represent ± one standard error.

current patterns, water levels, and increased temperatures) and watershed disturbances (flooding and sedimentation). Altered larval supply, habitat disturbance, and species interactions (e.g., predation and competition) offer several likely mechanisms for the patterns observed. Our analysis of long-term monitoring records is the first documentation of unique changes in estuarine species assemblage composition during El Niño conditions. Continuous monitoring and baseline data are essential to understand the ecology of these estuarine systems and their inherent variability over interannual-decadal time scales. This study also provides the groundwork for future empirical studies to clarify the relationship between El Niño events and species abundance patterns in estuarine habitats, and for developing predictive models to understand change and appropriately manage estuarine resources.

Episodic, El Niño-associated events may affect the composition of fish and invertebrate assemblages in southern California estuaries by modifying larval supply. Of the six new fish and invertebrate taxa appearing in our 1997–1998 collections, most were species with warm-water affinities commonly associated with coastal embayments in southern Baja California and the Gulf of California. Almost all specimens were first collected as juveniles that likely arrived at local estuarine habitats as planktonic larvae, riding northward with warm surface currents. During "typical" years, the southward flowing California current (0–200 m deep) carries most nearshore surface waters equator-ward, while coastal upwelling contributes to offshore transport (Parrish et al. 1981; Simpson 1984). However during "anomalous" El Niño years, upwelling is reduced and a poleward-flowing countercurrent dominates coastal flows, transporting warm, high salinity waters northward and displacing the California current offshore (Simpson

1984; Hayward et al. 1999). Long-duration, anomalous flow conditions can result in episodic pulses of planktonic eggs and/or larvae from southern sources, which are located "downstream" of southern California.

Flow anomalies account for the variable recruitment success of some coastal fisheries stocks (Parrish et al. 1981) and may be important in structuring nearshore benthic communities (Tegner and Dayton 1987). Because long-lived species naturally form age-structured populations and are persistent members of the community, size-frequency analysis provides one of the best indicators of recruitment events. *Paralabrax maculatofasciatus* (spotted sand bass), a long-lived (≤14 yrs) subtropical species that persists in warm-water bay refugia in southern California, displayed episodic recruitment pulses that matched peaks in summer sea-surface temperatures during 1984–85 and 1989–90 (Allen et al. 1995). High recruitment of *Semicossyphus pulcher* (sheephead) to temperate reefs at its northern distributional limit (Point Conception, CA) coincided with years of El Niño-associated variation in the coastal current regime (Cowen 1985). From our data we suggest that estuarine populations of *Mugil spp.,* another long-lived species (≤15 yrs; Hendricks 1961), also appear to be positively influenced by episodic larval recruitment events (Fig. 5). Furthermore, some portion of the *Mugil* spp. complex collected during our monitoring efforts may have been *Mugil curema,* a species also documented in California waters during the 1982–83 El Niño (Lea et al. 1988).

As ocean conditions transitioned to a cool-water, La Niña state in 1998 (Hayward et al. 1999), few warm-water species recruited to TE and LPL. Most of these species have ocean-going larvae which were likely exported offshore and carried southward by the California current, which was then in place. Recruitment did not occur despite reproductive output by some individuals that survived to maturity in local systems. For example, ovigerous female *Callinectes arcuatus* were observed on several dates (G. Williams, pers. obs.), but no juveniles were observed in local lagoons thereafter. However, reproducing individuals from these populations may have contributed larvae to other populations "downstream".

In the absence of additional recruitment events, persistence of many warmwater species appeared to be influenced by the longevity of individuals that recruited during the 1997–98 El Niño. Short-lived species (e.g., *Ctenogobius sagittula* and *Penaeus californiensis*) generally persisted for ≤6 months in estuaries, while longer-lived species (e.g., *Callinectes arcuatus* and *Petricola hertzana*) persisted and grew for more extended periods (up to 2 years). Persistence patterns suggest that these populations are ephemeral and depend on larval replenishment from elsewhere. Short persistence times for some of these tropical species may also be a result of rapid mortality due to low thermal tolerance. However, in our region hydrographic constraints on dispersal likely play a more important role than thermal tolerance in determining faunal distribution and persistence (Cowen 1985).

Changes in the abundance of two historically common benthic invertebrate species may be a response to El Niño-related flooding disturbance and sedimentation events rather than larval availability. *Grandidierella japonica,* an exotic disturbance-opportunist, exhibited extraordinary peaks in abundance following the winter floods, while populations of *Tagelus californiensis,* a native bivalve, plummeted in many areas. Similar impacts were observed at Mugu Lagoon in 1978, when flooding and sedimentation from winter storms resulted in long-term impacts to the distribution and composition of fish and invertebrate assemblages (Onuf and Quammen 1983, Onuf 1985). Sedimentation is an important factor that can lead to both gradual and abrupt changes in community dynamics in coastal estuaries (Onuf and Quammen 1983, Zedler et al. 1992, Desmond et al. in review). Immobile invertebrates in permanent burrows may be buried by catastrophic sedimentation events, leading to suffocation and mortality (Peterson 1985). In contrast, many epibenthic organisms (e.g., capitellid and spionid polychaetes, corophiid amphipods) opportunistically colonize newly deposited sediments, rapidly taking advantage of space and food resources (McCall 1977, Zajac and Whitlatch 1982, Levin et al. 1996).

Sedimentation rates appear to be considerably greater at TE than LPL (G. Williams, pers. obs.), perhaps due to differential levels of watershed disturbance and area (4403 km^2 and 420 km^2, respectively), and differences in impacts were reflected by benthic community responses. Mean sediment accretion on TE tidal mudflats during the winter of 1997–98 was over 8 cm, but reached levels of 12 cm in some areas (Ward 2000). This is higher than long-term TE marsh sedimentation rates of 1 cm yr^{-1} (Weis 1999), and dramatically more variable than East and Gulf coast sedimentation ranges of 0.1–1 cm yr^{-1} (Stevenson et al. 1986). Episodic sedimentation events illustrate the extreme influence which storms may have on Tijuana Estuary and point to a need to plan for long-term sediment management solutions (Zedler et al. 1992; Desmond et al. 1999). Furthermore, these impacts indicate the necessity of evaluating the possibilty of habitat shifts related to sedimentation events in future restoration efforts (Zedler 1996).

While the individual impacts of sedimentation and larval recruitment likely exerted major effects on estuarine assemblage composition, their combined, synergistic effects should not be ignored. Interspecific interactions with novel predators or competitors in disturbed habitats can substantially modify feeding patterns and abundance (Moyle et al. 1986, Moyle 1997). While storm-induced sedimentation events may have led to the rapid decline of *Tagelus californiensis* populations, predation by *Callinectes arcuatus* may have also played a role. *Callinectes arcuatus* are active, voracious predators of bivalves (Paul 1981), and the peak in crab abundance coincided with declines of *T. californiensis.* Similar declines in *Penaeus californiensis* numbers may be due to increased competition from *C. arcuatus* juveniles, which utilize similar resources and indirectly compete for food and space (Paul 1981). Related studies show that feeding patterns of some juvenile fish species (e.g., *Paralichthys californicus* and *Clevelandia ios*) shifted during El Niño years due to accompanying changes in prey abundance patterns at TE (G. Williams et al. in prep.).

This study provides an important record of faunal patterns and variability over interannual-decadal time scales. Furthermore, it suggests that some of southern California's coastal lagoon's may act as a north-south metapopulation for a number of fish and invertebrate taxa. Long-term datasets provided by biological monitoring programs are an irreplaceable resource that allows evaluation of subtle ecosystem responses to climatic cycles (e.g., El Niño events), anthropogenic impacts, exotic species invasions, and other events. Because southern California has an inherently variable environment, complete characterization of a 'normal' year is doubtful (Allen 1982, Desmond et al. in review). Thus, knowledge of temporal variability is needed to understand ecological patterns. Those who wish to test hypotheses about community membership, population structure, and species persistence in regions influenced by El Niño or other "events" will benefit from the continuation of long-term monitoring programs. In fact, researchers and resource managers cannot expect to understand today's assemblages or conserve their habitats without referring to records of historical composition and change.

Acknowledgments

This work was accomplished in cooperation with a large number of individuals over many years. We wish to thank the LPL Foundation and NOAA Sanctuaries and Programs division for funding ongoing monitoring efforts at LPL and TE, respectively, and the staff at Torrey Pines State Reserve and the Tijuana Estuary Visitor Center for their continued support. Julie Desmond, Sharook Madon, John Callaway, Robert Lea, Drew Talley, Camm Swift, and others encouraged this work, and their suggestions, ideas, and comments improved the manuscript.

Literature Cited

Allen, L. G. 1982. Seasonal abundance, composition, and productivity of the littoral fish assemblage in upper Newport Bay, California. U.S. Fish. Bull. 80:769–789.

Allen, L. G., T. E. Hovey, M. S. Love, and J. T. W. Smith. 1995. The life history of the spotted sand bass (*Paralabrax maculatofasciatus*) within the southern California bight. Calif. Coop. Oceanic Fish. Invest. Rep. 36:193–203.

Allen, L. G. 1998. Fisheries inventory and utilization of San Diego Bay, San Diego, California: 4th Annual Report, FY 1997–98. Prepared for U.S. Navy, Naval Facilities Engineering Command under Contract No. N68711-94-LT-4033, 25 pp.

Anderson, W. W. 1958. Larval development, growth, and spawning of the striped mullet (*Mugil cephalus*) along the south Atlantic coast of the U.S. U.S. Fish. Bull. 58:501–525.

Baker, J. C. 1979. A contribution to the life history of the yellowfin goby (*Acanthogobius flavimanus*) in the San Francisco Bay-Delta area. M.S. Thesis, California State University Sacramento, Sacramento, California, 36 pp.

Chapman, J. W., and J. A. Dorman. 1975. Diagnosis, systematics, and notes on *Grandidierella japonica* (Amphipoda: Gammaridea) and its introduction to the Pacific Coast of the United States. Bull. So. Calif. Acad. Sci. 74:104–108.

Charter, S. R. and H. G. Moser. 1996. Albulidae: Bonefishes. Pages 79–81 *in* H. G. Moser, editor. The early stages of fishes in the California Current region. California Cooperative Oceanic Fisheries Investigations Atlas no. 33., Marine Life Research Program, Scripps Institution of Oceanography, La Jolla, California, xii + 1505 pp.

Coan, E. V. 1997. Recent species of the genus *Petricola* in the Eastern Pacific (Bivalvia: Veneroidea). Veliger 40:298–340.

Cowen, R. K. 1985. Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: Causes and implications. J. Mar. Res. 43:719–742.

Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. Ecol. Applic. 8:309–322.

Dean, T. A., and F. R. Jacobsen. 1986. Nutrient-limited growth of juvenile kelp, *Macrocystis pyrifera*, during the 1982–1984 'El Niño' in southern California. Mar. Biol. 90:597–601.

De La Cruz-Aguero, J., and V. M. Cota-Gomez. 1998. Ictiofauna de la laguna de San Ignacio, Baja California Sur, Mexico: nuevos registros y ampliaciones de ambit. Ciencias Marinas 24:353–358.

Desmond, J. S., D. H. Deutschman, and J. B. Zedler. In review. Fish and invertebrate community structure in three southern California estuaries: An 11-year study. Submitted to Estuaries.

Desmond, J., M. Cordrey, J. Johnson, K. Ward, and J. Zedler. 2000. Tijuana River National Estuarine Research Reserve: Annual report on ecosystem monitoring. NOAA Technical Memorandum on the Tijuana River National Estuarine Research Reserve. NOAA National Ocean Service, Sanctuaries and Programs Division. Washington D.C., 60 pp.

Desmond, J., G. Williams, M. James, J. Johnson, J. Callaway, and J. Zedler. 1999. Tijuana River

National Estuarine Research Reserve: Annual report on ecosystem monitoring. NOAA Technical Memorandum on the Tijuana River National Estuarine Research Reserve. NOAA National Ocean Service, Sanctuaries and Programs Division, Washington D.C., 67 pp.

Dore, I., and C. Frimodt. 1987. An illustrated guide to shrimp of the world. Van Nostrand Reinhold. New York, New York, 229 pp.

Duggan, R. M. 1989. The bivalve community and role of *Laevicardium substriatum* in the Tijuana Estuary. M. S. Thesis, San Diego State University, San Diego, California, 131 pp.

Emmett, R. L., S. L. Stone, S. A. Hinton, and M. E. Monaco. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries. Volume II: Species life history summaries. ELMR Rep. No. 8. NOAA/NOS Strategic Environmental Assessments Division, Rockville, Maryland, 329 pp.

Follett, W. I. 1960. The fresh-water fishes—their origin and affinities. Symposium on the biogeography of Baja California and adjacent seas. Syst. Zool. 9(3–4):212–232.

Garth, J. S., and W. Stephenson. 1966. Brachyura of the Pacific coast of America, Brachyrhyncha: Portunidae. Allan Hancock Monographs in Mar. Biol. 1:1–154.

Greenstein, D. J., and L. L. Tiefenthaler. 1997. Reproduction and population dynamics of a population of *Grandidierella japonica* (Stephensen) (Crustacea: Amphipoda) in Upper Newport Bay, California. Bull. So. Calif. Acad. Sci. 96:34–42.

Haston, L., and J. Michaelsen. 1994. Long-term central coastal California precipitation variability and relationships to El Niño-Southern oscillation. J. Climate 7:1373–1387.

Hayward, T. L., T. R. Baumgartner, D. M. Checkley, R. Durazo, G. Gaxiola-Castro, K. D. Hyrenbach, A. W. Mantyla, M. M. Mullin, T. Murphree, F. B. Schwing, P. E. Smith, and M. J. Tegner. 1999. The state of the California current in 1998–1999: Transition to cool-water conditions. Calif. Coop. Oceanic Fish. Invest. Rep. 40:29–62.

Hendricks, L. J. 1961. The striped mullet, *Mugil cephalus* Linnaeus. Pp. 95–103 *in* The ecology of the Salton Sea, California, in relation to the sportfishery (B. W. Walker, ed.), California Dept. Fish and Game, Fish Bulletin 113, 204 pp.

Horn, M. and L. Allen. 1985. Fish community ecology in southern California bays and estuaries. Pages 169–190 *in* Fish community ecology in estuaries and coastal lagoons: Toward an ecosystem integration (A. Yañez Arancibia, ed.), UNAM Press, México.

Hubbs, C. L. 1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. J. Mar. Res. 7:459–482.

Hubbs, C. L., and L. P. Schulz. 1929. The northward occurrence of southern forms of marine life along the Pacific Coast in 1926. Calif. Fish Game 15:234–241.

Kahya, E., and J. A. Dracup. 1994. The influences of Type 1 El Niño and La Niña events on streamflows in the Pacific southwest of the United States. J. Climate 7:965–976.

Karpov, K. A., D. P. Albin, and W. H. Van Buskirk. 1995. The marine recreational fishery in northern and central California: A historical comparison (1958–86), status of stocks (1980–86), and effects of changes in the California Current. California Dept. Fish and Game, Fish Bulletin 176, 192 pp.

Ketchen, K. S. 1956. Climatic trends and fluctuations in yield of marine fisheries of the Northeast Pacific. Fish. Res. Board Canada 13:357–374.

Lea, R. N., C. C. Swift, and R. J. Lavenberg. 1988. Records of *Mugil curema* Valenciennes, the white mullet, from southern California. Bulletin of the Southern California Academy of Sciences. 87(1):31–34.

Levin, L. A., D. Talley, and G. Thayer. 1996. Succession of macrobenthos in a created salt marsh. Marine Ecology Progress Series 141:67–82.

Los Peñasquitos Lagoon Foundation and State Coastal Conservancy. 1985. Los Penasquitos Lagoon enhancement plan and program. A California State Coastal Conservancy publication, 119 pp.

Lynn, R. J., T. Baumgartner, J. Garcia, C. A. Collins, T. L. Hayward, K. D. Hyrenbach, A. W. Mantyla, T. Murphree, A. Shankle, F. B. Schwing, K. M. Sakuma, and M. J. Tegner. 1999. The state of the California current, 1997–1998: Transition to El Niño Conditions. Calif. Coop. Oceanic Fish. Invest. Rep. 39:25–49.

Magallon-Barajas, F. J. 1987. The Pacific shrimp fishery of Mexico. Calif. Coop. Oceanic Fish. Invest. Rep. 28:43–52.

Marcus, L. 1989. The coastal wetlands of San Diego County. California State Coastal Conservancy publication, 64 pp.

Massey, B. W., D. W. Bradley, J. L. Atwood. 1992. Demography of a California least tern colony including effects of the 1982–1983 El Niño. Condor 94(4):976–983.

McCall, P. L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. Mar. Res. 35:221–261.

McGoodwin, J. R. 1979. The decline of Mexico's Pacific inshore fisheries. Oceanus 22(2):51–59.

McLean, J. H. 1969. Marine shells of southern California. Los Angeles County Museum of Natural History Science Series 24, Zoology No. 11, 104 pp.

Merino, J. 1981. A study of the temperature tolerances of adult *Solen rosaceus* and *Tagelus californianus* in south San Diego Bay: the effects of power plant cooling water discharge. Ph.D. Dissertation, San Diego State University, San Diego, California, 140 pp.

Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Fish Bulletin 157, 249 pp.

Mojica, R., J. M. Shenker, C. W. Harnden, and D. E. Wagner. 1994. Recruitment of bonefish *Albula vulpes,* around Lee Stocking Island, Bahamas. Fish. Bull. 93:666–674.

Morales-Bojorquez, E., and J. Lopez-Martinez. 1999. Brown shrimp fishery in the Gulf of California. Calif. Coop. Oceanic Fish. Invest. Rep. 40:28.

Morris, R. H., D. P. Abbott, and E. C. Haderlie. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, California, 690 pp.

Moser, H. G., R. L. Charter, P. E. Smith, D. A. Ambrose, S. R. Charter, C. A. Meyer, E. M. Sandknop, and W. Watson. 1993. Distributional atlas of fish larvae in the California Current region: taxa with less than 1000 total larvae, 1951 through 1984. CalCOFI Atlas No. 31-32. Marine Life Research Program, Scripps Institution of Oceanography, La Jolla, California, xxix + 223 pp.

Moyle, P. B. 1997. Fish invasions in California: Do abiotic factors determine success? Ecology 77: 1666–1670.

Moyle, P. B., R. A. Daniels, B. Herbold and D. Baltz. 1986. Patterns in distribution and abundance of a noncoevolved assemblage of estuarine fishes in California. U.S. Fish. Bull. 84:105–117.

Nordby C. S. and J. B. Zedler. 1991. Responses of fish and macrobenthic assemblages to hydrologic disturbances in Tijuana Estuary and Los Peñasquitos Lagoon, CA. Estuaries 14:80–93.

Onuf, C. P. 1985. The ecology of Mugu Lagoon, California: An estuarine profile. U.S. Fish and Wildlife Service Biological Report 85. 122 pp.

Onuf, C. P. and M. L. Quammen. 1983. Fishes in a California coastal lagoon: effects of major storms on distribution and abundance. Mar. Ecol. Prog. Ser. 12:1–14.

Parrish, R. H., C. S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California current. Biol. Ocean. 1(2):175–203.

Paul, R. K. G. 1981. Natural diet, feeding, and predatory activity of the crabs *Callinectes arcuatus* and *C. toxotes* (Decapoda, Brachyura, Portunidae). Mar. Ecol. Prog. Ser. 6:91–99.

Paul, R. K. G. 1982a. Observations on the ecology and distribution of swimming crabs of the genus *Callinectes* (Decapoda, Brachyura, Portunidae) in the Gulf of California, Mexico. Crustaceana 42:96–100.

Paul, R. K. G. 1982b. Abundance, breeding, and growth of *Callinectes arcuatus* Ordway and *Callinectes toxotes* Ordway (Decapoda, Brachyura, Portunidae) in a lagoon system on the Mexican Pacific coast. Estuar. Coast. Shelf Sci. 14:13–26.

Peterson, C. H. 1985. Patterns of lagoonal bivalve mortality after heavy sedimentation and their paleoecological significance. Paleobiology 11:139–153.

Pfeiler, E. 1981. Salinity tolerance of leptocephalous larvae and juveniles of the bonefish (Albulidae: *Albula*) from the Gulf of California. J. Exp. Mar. Biol. Ecol. 52:37–45.

Pfeiler, E. 1984. Inshore migration, seasonal distribution and sizes of larval bonefish, *Albula,* in the Gulf of California. Environ. Biol. Fishes 10:117–122.

Pfeiler, E., M. A. Mendoza, and F. A. Manrique. 1988. Premetamorphic bonefish (*Albula* sp.) leptocephali from the Gulf of California with comments on life history. Environ. Biol. Fishes 21: 241–249.

Radovich, J. 1961. Relationships of some marine organisms of the Northeast Pacific to water temperatures, particularly during 1957 through 1959. Calif. Dept. Fish and Game, Fish Bull. No. 112, 62 pp.

Rhoads, D. C., P. L. McCall, and J. Y. Yingst. 1978. Disturbance and production on the estuarine seafloor. Am. Scientist 578:577–586.

Rosales-Casian, J. A. 1996. Ictiofauna de la Bahia San Quintin, Baja California, Mexico, y su costa adjacente. Ciencias Marinas 22:443–458.

Ruiz-Campos, G., and J. L. Castro-Aguirre. 1999. First records of two tropical gobies, *Awaous tajasica* and *Ctenogobius sagittula* (Pisces: Gobiidae), in the continental waters of Baja California, Mexico. Bull. So. Calif. Acad. Sci. 98:131–136.

Sandknop, E. M., and W. Watson. 1996. Mugilidae: Mullets. Pp. 1078–1081 *in* H. G. Moser, editor. The early stages of fishes in the California Current region. California Cooperative Oceanic Fisheries Investigations Atlas no. 33., Marine Life Research Program, Scripps Institution of Oceanography, La Jolla, California, xii + 1505 pp.

Schonher, T. and S. E. Nicholson. 1989. The relationship between California rainfall and ENSO events. J. Climate. 2:1258–1269.

Simpson, J. J. 1984. El Niño-induced onshore transport in the California current during 1982–83. Geophys. Res. Let. 11(3):233–236.

Snyder-Conn, E., and R. C. Brusca. 1975. Shrimp population dynamics and fishery impact in the northern Gulf of California. Ciencas Marinas 2(2):54–67.

Squire, J. L. 1987. Relation of sea surface temperature changes during the 1983 El Niño to the geographical distribution of some important recreational pelagic species and their catch temperature parameters. Mar. Fish. Rev. 49(2):44–57.

Stevenson, J. C., L. G. Ward, and M. S. Kearney. 1986. Vertical accretion in marshes with varying rates of sea level rise. Pp. 241–259 *in* Estuarine Variability (D. A. Wolfe, ed.), Academic Press, Inc., Orlando, Florida, 509 pp.

Swift, C. C., T. R. Haglund, M. Ruiz, and R. N. Fisher. 1993. The status and distribution of the freshwater fishes of Southern California. Bull. So. Calif. Acad. Sci. 92:101–167.

Talley, D. M. 2000. Ichthyofaunal utilization of newly-created versus natural salt-marsh creeks in Mission Bay, CA. Wetlands Ecol. Mgmt. 8:117–132.

Tegner, M. J., and P. K. Dayton. 1987. El Niño effects on southern California kelp forest communities. Adv. Ecol. Res. 17:243–279.

Usui, C. A. 1981. Behavioral, metabolic, and seasonal size comparisons of an introduced gobiid fish, *Acanthogobius flavimanus,* and a native cottid, *Leptocottus armatus,* from upper Newport Bay, California. M.S. Thesis, California State University Fullerton, California, ix + 52 pp.

Veit, R. R., P. Pyle, and J. A. McGowan. 1996. Ocean warming and long-term change in the pelagic bird abundance within the California Current system. Mar. Ecol. Prog. Ser. 139:11–18.

Walford, L. A. 1931. Northward occurrence of southern fish off San Pedro in 1931. Calif. Fish Game 17(4):401–405.

Ward, K. M. 2000. Episodic colonization of an intertidal mudflat by cordgrass (*Spartina foliosa*) at Tijuana Estuary. M. S. Thesis, San Diego State University, San Diego, California, viii + 103 pp.

Weis, D. A. 1999. Vertical accretion rates and heavy metal chronologies in wetland sediments of Tijuana Estuary. M. S. Thesis, San Diego State University, xi + 106 pp.

Williams, A. B. 1974. The swimming crabs of the genus *Callinectes.* Fish. Bull. 72:685–798.

Williams, G. D., J. Desmond, and J. Zedler. 1998a. Extension of two nonindigenous fishes, *Acanthogobius flavimanus* and *Poecilia latipinna,* in San Diego Bay marsh habitats. Calif. Fish Game 84:1–17.

Williams, G. D., G. Noe, and J. Desmond. 1998b. The physical, chemical, and biological monitoring of Los Peñasquitos Lagoon. Annual report submitted to the Los Peñasquitos Lagoon Foundation. Pacific Estuarine Research Lab, San Diego State University, San Diego, California, 47 pp.

Williams, G. D., J. West, M. Cordrey, and K. Ward. 1999a. The physical, chemical, and biological monitoring of Los Peñasquitos Lagoon. Annual report submitted to the Los Peñasquitos Lagoon Foundation. Pacific Estuarine Research Lab, San Diego State University, San Diego, California, 47 pp.

Williams, G. D., J. Callaway, M. Wells, J. Jackson. 1999b. Monitoring and managing Los Peñasquitos Lagoon's biological resources: Effects of a rapidly changing watershed. *in* Coastal Zone 99: Abstracts of Presentations. July 27–29, 1999, San Diego, California, USA.

Zajac, R. N., and R. B. Whitlatch. 1982. Responses of estuarine infauna to disturbance II. Spatial and temporal variation of succession. Marine Ecology Progress Series 10:15–27.

Zedler, J. B., C. S. Nordby, and B. E. Kus. 1992. The ecology of Tijuana Estuary, California: A

National Estuarine Research Reserve. NOAA Office of Coastal Resource Management, Sanctuaries and Reserves Division, Washington, D. C. ii + 151 pp.

Zedler, J. B. Principal author. 1996. Tidal wetland restoration: A scientific perspective and southern California focus. California Sea Grant College System, University of California, La Jolla, California. Report No. T-038. vi + 129 pp.

Accepted for publication 21 December 2000.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 238–248

New Range Records of 12 Marine Invertebrates: The Role of El Niño and Other Mechanisms in Southern and Central California

Steve I. Lonhart[1]* and Jeff W. Tupen[2]

[1]*Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064, USA*
[2]*Morro Group, Inc., 1422 Monterey St., Suite C200, San Luis Obispo, CA 93401*

Abstract.—The occurrence of marine organisms northward of their known range limit along the eastern Pacific during El Niño Southern Oscillation (ENSO) events is an increasingly well-studied phenomenon. However, in addition to ENSO related range extensions, there are several mechanisms potentially contributing to the occurrence and persistence of extralimital populations. We report 12 new records of intertidal or shallow subtidal marine invertebrates (11 mollusks and 1 brittle star) along the southern and central coast of California. The 1997–98 ENSO event accounted for only one of these records, although previous ENSO events presumably contributed to the nine remaining northward records. Other mechanisms, such as thermal refugia and sampling artifacts, provide more likely explanations for nine of the northern and both of the southern new records.

The ephemeral occurrence of marine organisms extending beyond their typical geographic range is a well-documented effect of El Niño Southern Oscillation (ENSO) conditions along the eastern Pacific coast of North America (e.g., Wooster and Fluharty 1985; Glynn 1990). During 1982–83 and 1997–98, the two strongest ENSO events of the 20th century (McPhaden 1999) caused large scale northward shifts of tropical and warm-temperate marine species along the eastern Pacific (Pearcy and Schoener 1987; McGowan et al. 1998). Among the various oceanographic effects of an ENSO event along the coast of California, the strengthening of the poleward flowing Davidson Current (Glynn 1961; Thurman 1985) is arguably the greatest contributor to changes in distribution of coastal marine organisms. As this countercurrent builds, fishes actively track the warm water (Radovich 1960), and plankton, including the larvae of benthic organisms, passively drift northward along the coast (Pearcy and Schoener 1987).

For most marine organisms these northward excursions are ephemeral, with southern species disappearing soon after oceanic conditions return to normal (Pearcy and Schoener 1987; Dayton and Tegner 1990; Richmond 1990). In addition to these ephemeral occurrences, ENSO events also may either establish relict populations or sustain marginal populations. Relict populations, as used here, are disjunct from southern source populations and persist for one generation in areas influenced by the ENSO event. Marginal populations are also disjunct from southern populations but persist as long as ENSO events or other mechanisms allow recruitment (i.e., they act as "sinks"). However, besides these ENSOmediated changes in geographic range, there are several other mechanisms potentially contributing to the detection, occurrence, and persistence of extralimital populations.

---

* Corresponding author.

We discuss 12 new range records of marine invertebrates along the southern and central coast of California. For each species, we present evidence to address whether or not these new records are the result of ENSO events, and discuss other mechanisms such as localized thermal anomalies associated with the thermal plumes of coastal power plants and sampling artifacts.

Methods

Specimens were collected by the authors from Monterey Bay (SIL), Morro Bay (JWT), Diablo Canyon (JWT), and Santa Catalina Island (SIL), California (Fig. 1), spanning a latitudinal distance of 550 km. We collected specimens from eight sites characterized as either intertidal rocky benches or subtidal ($\leq$20 m) kelp forests on rocky reefs. Many of the specimens from Diablo Canyon were collected at permanent intertidal and subtidal stations during a 24 yr study on the effects of the Diablo Canyon Nuclear Power Plant (DCPP) on the marine environment. Details of the spatial and temporal sampling design are provided elsewhere (Tenera 1997). Collections in Monterey Bay and at Santa Catalina Island were made at study sites selected for other projects. Species were identified initially by the authors, verified by taxonomic specialists at natural history museums, and voucher specimens were deposited at one of the following California museums: Natural History Museum of Los Angeles County (LACM), Santa Barbara Museum of Natural History (SBMNH), and California Academy of Sciences (CAS) (Table 1).

The known geographic range for each species was compiled from commonly used field guides (Abbott 1974; McLean 1978; Morris et al. 1980; Behrens 1991; Coan et al. 2000), by personal inspection of museum collections at SBMNH and CAS, and from searches of museum collections by curators at the LACM, San Diego Natural History Museum (SDNHM), Academy of Natural Sciences, Philadelphia (ANSP), and the Delaware Museum of Natural History (DMNH). Unpublished range records discovered during inspection of museum collections that exceeded our field data are also included.

Nomenclature follows McLean (1978) and Morris et al. (1980). Intertidal elevations in meters (m) are relative to mean lower low water (MLLW).

Results

We collected 12 species of eastern Pacific coastal marine invertebrates (11 mollusks and 1 brittle star) at sites beyond their published geographic ranges (Table 1), with ten records northward and two southward. At our study sites, extralimital populations of four species (*Ophiactis simplex, Musculus pygmaeus, Norrisia norrisi,* and *Nucella canaliculata*) were well established, with evidence of multiple size-classes or local reproduction. For the remaining eight species, relatively few specimens were observed and there was no evidence of local reproduction, which suggests these represent either ephemeral occurrences or relict populations. We present results separately for each species. Table 1 summarizes the broadest extent of occurrence for each species based on either our collections or unpublished museum material, whichever was more extensive.

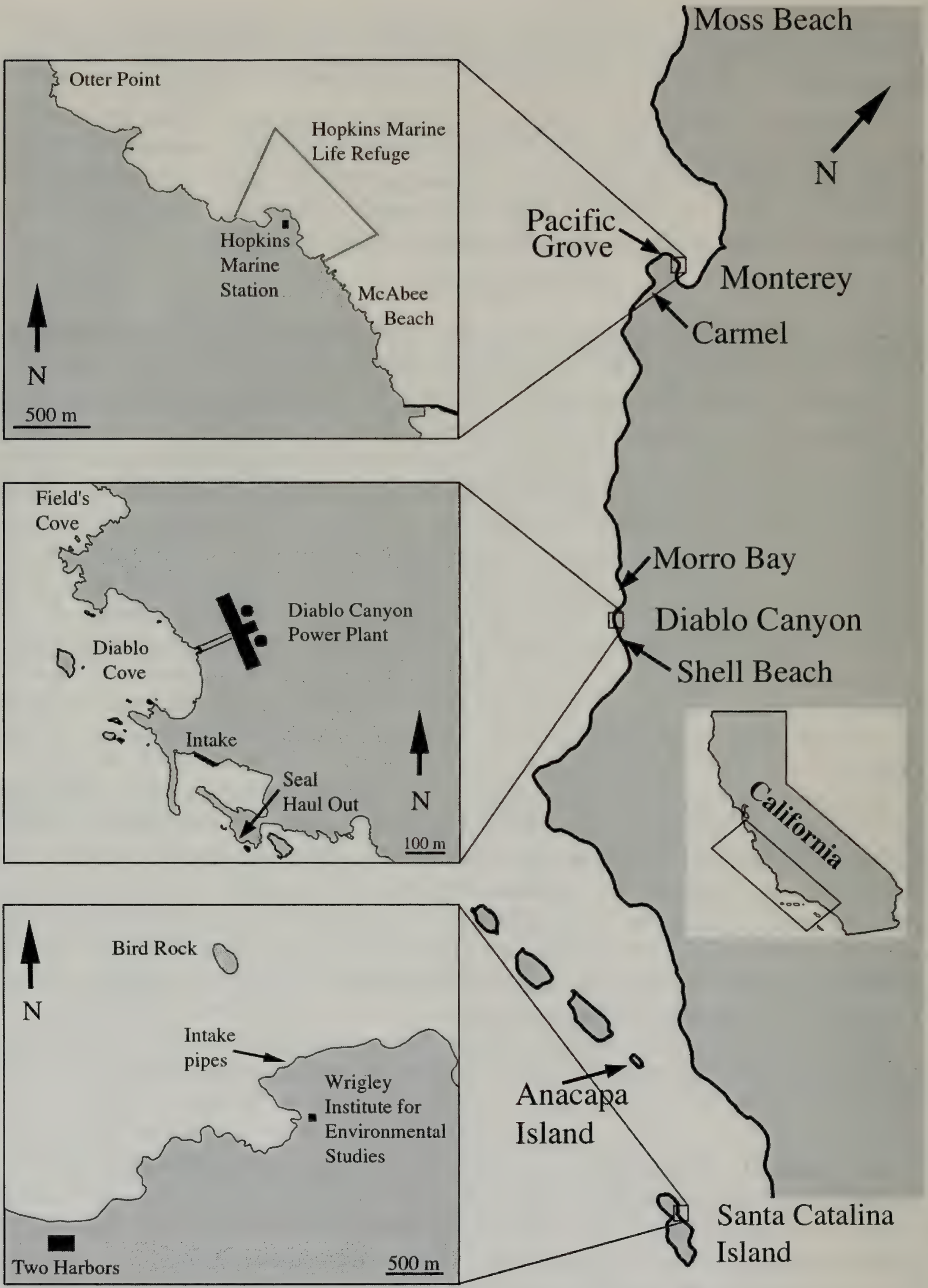

Moss Beach
N
Pacific Grove
Monterey
Carmel
Morro Bay
Diablo Canyon
Shell Beach
California
Anacapa Island
Santa Catalina Island
Otter Point
Hopkins Marine Life Refuge
Hopkins Marine Station
McAbee Beach
N
500 m
Field's Cove
Diablo Canyon Power Plant
Diablo Cove
Intake
Seal Haul Out
N
100 m
Bird Rock
N
Intake pipes
Wrigley Institute for Environmental Studies
Two Harbors
500 m

Fig. 1. Location of study sites and new range records along the coast of California, USA.

Table 1. Species, published range, new record of occurrence, direction and distance, reproductive mode and references, and voucher material for 12 coastal marine invertebrates collected along the northeastern Pacific. Key: N, northern record; S, southern record; B, nonplanktonic larva; P, planktonic larva; P/B, both; ?, presumed larval type based on closely related species. See Methods for museum abbreviations; voucher material consists of one specimen unless noted otherwise (no.).

Taxon		New record			Reproduction		
Species	Published range*	To	Dir.	km	Larvae	Ref.‡	Voucher material
Prosobranchia							
Norrisia norrisi	Isla Asuncion, BCS to Point Conception, CA	Monterey	N	432	P	5	ANSP 388241
Trivia solandri	Panama to Palos Verdes, CA	Pacific Grove	N	640	P	5	LACM 59-12.50
Opalia funiculata	Panama to Santa Monica, CA	Moss Beach	N	720			CAS 116964
Maxwellia gemma	Baja California to Santa Barbara, CA	McAbee Beach	N	432	B?	5	LACM 152452
M. santarosana	Baja California to Morro Bay, CA	McAbee Beach	N	320	B?	5	LACM 152451 (2), CAS 112494 (2)
Nucella canaliculata	Cayucos, CA to Alaska	Shell Beach	S	48	B	5	CAS 116961
Pteropurpura festiva	Baja California to Point Conception, CA	Morro Bay	N	240	P	4	LACM 152587, 152588
Heterobranchia							
Odostomia eucosmia	Baja California to Palos Verdes, CA	Carmel	N	640	P	2	LACM 81–47
Turbonilla kelseyi	Baja California to Santa Barbara, CA	Diablo Canyon	N	112	P/B	3	LACM 152442–152445
Opisthobranchia							
Polycera alabe	Gulf of California to Cedros Island, BCN	Anacapa Island	N	302	P	1	Slides at CAS
Bivalvia							
Musculus pygmaeus	Dillon Beach, CA to Cayucos†, CA	Diablo Cove	S	32	B	6	SBMNH 144900 (20), 144901 (20)
Ophiuroidea							
Ophiactis simplex	Panama to Santa Cruz Island, CA	Morro Bay	N	240	P/B	5	LACM 99-024.001 (40)

* BCS is Baja California Sur and BCN is Baja California Norte.

‡ References: 1, Behrens (1991); 2, Collin and Wise (1997); 3, Cumming (1993); 4, Fotheringham (1971); 5, Morris et al. (1980); 6, Coan et al. (2000).

† The southern limit of *Musculus pygmaeus* in Coan et al. (2000) is based on the specimens collected during this study.

Norrisia norrisi.—Norris' topsnail is relatively common in Diablo Cove (35°12′40″N, 120°51′25″W; Tenera 1997). Juveniles were collected within the intertidal red alga *Gastroclonium subarticulatum* in summer/fall 1993 and summer 1994. Large snails (to 45 mm) were first observed subtidally in Diablo Cove in 1991 (Tenera 1997). By 1998, *Norrisia* was commonly observed (>20 snails per dive) on the subtidal stipitate kelps *Pterygophora californica* and *Macrocystis pyrifera* in Diablo Cove. Despite this local abundance, *Norrisia* has not been observed subtidally or intertidally at adjacent locations outside of Diablo Cove (Tenera 1997). Four lots (LACM 152433 through 152436, all 1993 except 152434, 1991) of one juvenile each from the intertidal zone (+0.3 m) of Diablo Cove were deposited as voucher material. Museum specimens establish that *N. norrisi* has occurred, at least sporadically, north of Point Conception since the late 1800's (ANSP 319023, likely pre-1900, Monterey, California; ANSP 388241, undated, Monterey, California; LACM 46-35.8, 1946, north of Cayucos, California). Data and a discussion of conflicting published range limits for *Norrisia* are presented elsewhere (Lonhart and Tupen in prep.).

Trivia solandri.—Five live and several freshly dead shells of Solander's trivia have been collected since 1986 at Diablo Canyon. In April 1999, a single 18 mm specimen (LACM 152582, 1999) was collected by J. Carroll at a depth of 3 m in Diablo Cove. Between 1959–1964, J. McLean collected a single shell (LACM 59-12.50) intertidally at Pacific Grove, Monterey County, California, which represents the northern-most record of occurrence.

Opalia funiculata.—The scalloped wentletrap is a gastropod that parasitizes large anthozoans (Morris et al. 1980). In July 1993, a single intertidal specimen (12.8 mm) associated with the tubiculous polychaete *Pista elongata* was collected in Diablo Cove. In July 1999, two additional individuals (19.7 and 15.5 mm) were collected in Diablo Cove on an intertidal (0 m) *Anthopleura elegantissima.* All three were deposited as voucher specimens (LACM 152437, 1993; LACM 152583, 1999). Unpublished museum material was collected at Cayucos, San Luis Obispo County, California (LACM 128091, undated; SBMNH 145295, 1966) and at Moss Beach, San Mateo County, California (CAS 116964, 1947). The single specimen from Moss Beach is the northern-most record of occurrence.

Maxwellia gemma.—In 1998, a single specimen (33.2 mm) of the gem murex was collected subtidally (17 m depth) at McAbee Beach (Fig. 1; 36°37′00″N, 121°53′45″W) and deposited as voucher material (LACM 152452, 1998). In May 2000, a second snail (33 mm) at this site was observed but not collected.

Maxwellia santarosana.—Since 1996, the Santa Rosa murex has been observed or collected nine times in Monterey Bay at depths from 10 to 17 m. In 1996, a large (>30 mm) snail was observed in a kelp forest at Otter Point (36°37′45″N, 121°55′15″W). Five months later, a single adult was observed in the Hopkins Marine Life Refuge (HMLR; 36°37′18″N, 121°54′10″W), 2 km southeast of Otter Point. In 1997, a third snail was observed on an offshore pinnacle within 1 km of Otter Point. In 1998 at McAbee Beach, one specimen (32.1 mm) was collected amidst filamentous red algae covering a patch of rocky reef and a second specimen (32.4 mm) was collected on a large boulder; two additional snails were observed at McAbee Beach later that year. In 1999, a 32.5 mm snail was observed at HMLR on a rocky reef and a second snail (31.6 mm) collected at McAbee Beach was eating the vermetid snail *Petaloconchus montereyensis.* Four snails from McAbee

Beach were deposited as voucher material (2 in CAS 112494, 1998; 2 in LACM 152451, 1998).

Nucella canaliculata.—The channeled dogwhelk is fairly abundant but patchy (about 1–3/m^2) at Seal Haul Out, a rocky intertidal bench (+0.9 m) near the DCPP intake facility characterized by cooler than normal surface temperatures due to a steep slope (Tenera 1997). Snails at this site are commonly nestled among California mussels (*Mytilus californianus*), a common prey item. The presence of egg capsules, from which crawl-away juveniles emerge, and the persistence of multiple size-classes suggest this population is self-sustaining. Twenty snails were deposited as voucher material (LACM 152447, 1998). Unpublished museum material (a single, live-collected specimen CAS 116961, 1969) collected from Shell Beach, San Luis Obispo County, California represents the southern-most record of occurrence.

Pteropurpura festiva.—In May 1998, the first observation of the festive murex in Diablo Cove was a large, subtidal (3 m depth) individual next to vase-shaped egg capsules. This species was absent from samples taken between 1976–95 (Tenera 1997). Since 1998, eight large specimens (≥30 mm) have been observed in Diablo Cove, with a single 43.3 mm specimen deposited as voucher material (LACM 152446, 1998). Subtidal searches in the Morro Bay Power Plant discharge canal (12 km northward of Diablo Cove; 35°22′16″N, 120°51′57″W) from 1991 to 1998 produced no specimens. However, in November 1999, a single 45.5 mm *P. festiva* was collected from the discharge canal by M. Behrens and deposited as voucher material (LACM 152588). Several museum specimens were collected from Morro Bay (DMNH 18216.3, undated; SBMNH 110345, 1939; CAS 116957 through 116959, unrelated lots, all undated). Data and a discussion of conflicting published range limits for *Pteropurpura* are presented elsewhere (Lonhart and Tupen in prep.).

Odostomia eucosmia.—During 1980–1995, 19 specimens of this small (to 3 mm) shelled heterobranch were collected within the intertidal (+0.3 m) red alga *Gastroclonium subarticulatum* at Diablo Canyon: 11 of these were from Diablo Cove and 8 were from Field's Cove (35°12′56″N, 120°51′30″W), which is approximately 1 km upcoast of Diablo Cove. Four specimens, ranging in shell height from 1.7 to 2.4 mm, were deposited as vouchers (LACM 152438 through 152441, all 1993 except 152439, 1987). In 1981, J. McLean collected a single specimen (LACM 81-47) of *O. eucosmia* at Carmel, Monterey County, California, which represents the northern-most record of occurrence.

Turbonilla kelseyi.—During 1980–1995, only two specimens were collected from Field's Cove, but 82 were found in Diablo Cove. Most of the specimens (n=57) from both intertidal sites (+0.3 m) were associated with the intertidal red alga *Gastroclonium subarticulatum,* and the rest with either the fleshy red alga *Chondracanthus canaliculatus* or the coralline alga *Corallina vancouveriensis.* Four voucher specimens (LACM 152442 through 152445, all 1981 except 152445, 1993) ranged in size from 2.6 to 3.6 mm.

Polycera alabe.—In May 1998, two specimens of *P. alabe* were collected in kelp forest habitat (33°26′53″N, 118°28′45″W) near the Wrigley Institute for Environmental Studies on Santa Catalina Island (Fig. 1). These strikingly colored nudibranchs—readily distinguished from congeners by their elongate papillae and dark pigmentation—were collected off the bryozoan *Bugula neretina* at 6 m depth near the intake pipes (Fig. 1). Species verifications were made by Gary McDonald (UCSC Long Marine Laboratory) viewing live specimens and by Terry Gosliner (CAS) viewing slide material. None of the specimens were preserved as voucher material but slides were deposited at CAS. Specimens observed at Anacapa Island in 1998 (D. Richards personal communication) represent the northern-most record of occurrence.

Musculus pygmaeus.—The Monterey dwarf-mussel is a very small (to 4.5 mm) bivalve, almost exclusively found attached to the red alga *Endocladia muricata* within the mid- to high-intertidal zone (+0.9 m). During 1980–95, measured densities of this brooding mussel reached 86600/m^2 within *E. muricata* in Diablo Cove and consisted of many sizes (range 0.5–4 mm). Two lots of 20 individuals from Field's Cove and Diablo Cove were deposited as voucher specimens (SBMNH 144900 and 144901, respectively, 1993).

Ophiactis simplex.—In 1991 in Diablo Cove (Fig. 1), several specimens of this small (2–6 mm disk diameter), six-armed brittle star were collected from the rhizomatous holdfasts of the intertidal (+0.3 m) red alga *Gastroclonium subarticulatum.* Fewer specimens were also collected within vacant sand tubes of the polychaete *Phragmatopoma californica* and vacant micromollusk shells (typically *Alia* spp. and *Lacuna* spp.). By 1993, *O. simplex* density in Diablo Cove increased to 7200/m^2 (Tenera 1997). Subtidal specimens were also abundant and generally larger than intertidal specimens, and typically occupied rock fissures or holdfasts of foliose red algae such as *Gymnogongrus linearis.* Subtidal brittle stars were restricted to areas and depths of the cove with elevated temperatures (generally ≤3 m depth). In August 1999, *O. simplex* was found 12 km northward of Diablo Cove within the thermal discharge canal of the Morro Bay Power Plant at Estero Bay, where abundance estimates reached 5000/m^2. Seven intertidal (+0.3 m) and nine subtidal (3 m depth) specimens from Diablo Cove were deposited as voucher material (LACM 93-174.1, 1993 and 98-37.1, 1998, respectively), as were 40 specimens from Estero Bay (LACM 99-024.001, 1999).

Discussion

Four of the 12 species presented in this study have established marginal populations beyond their known geographic range, while the remaining eight species may represent either relict populations or ephemeral occurrences. Four species (*Norrisia norrisi, Nucella canaliculata, Musculus pygmaeus,* and *Ophiactis simplex*) have established marginal populations that are consistently abundant at our study sites, and the density and size structure of these four species are similar to those found within their known geographic range. Further study is needed to determine if *N. norrisi* and *O. simplex* populations in Diablo Cove are sustained by local reproduction or by larvae from southern California. Of the eight remaining species, four (*Maxwellia gemma, M. santarosana, Odostomia eucosmia,* and *Turbonilla kelseyi*) were uncommon at their new range limits but consistently found over multiple years. Since only large adults were observed and there was no evidence of recruitment, these four species may represent ENSO-related relict populations. The remaining four species (*Opalia funiculata, Polycera alabe, Pteropurpura festiva,* and *Trivia solandri*) were rarely found, with only two to several individuals observed over multiple years.

Environmental conditions and ecological processes constantly modify the temporal and spatial extent of a species (Brown et al. 1996). In marine ecosystems, the rate of geographic expansion has accelerated (Elton 1958; Vermeij 1991; Cohen and Carlton 1998) due primarily to anthropogenic introductions via ship ballast water (Carlton and Geller 1993). Natural transport mechanisms, such as larval dispersal by oceanic currents, are unlikely contributors to range expansions during normal oceanic conditions. However, anomalous currents generated during an ENSO event have the potential to transport pulses of recruits to areas beyond a species' known geographic range. In addition to anthropogenic introductions and recent ENSO events as dispersal mechanisms, other factors, such as habitat modification due to climate change or thermal effluent, and search artifacts, may also explain these new range records.

ENSO Events

During an ENSO event, countercurrents (e.g., Davidson Current) strengthen along the northeastern Pacific (Norton et al. 1985), moving warm, nutrient-poor water poleward. In general, there are three range-related consequences of this anomalous circulation pattern along coastal California. First, ephemeral occurrences of sub-tropical and warm-temperate species are noted as organisms move well beyond their typical northern range limits. This is the most well known consequence and there are numerous published reports of organisms, such as fishes, that track the warm water as it flows northward (e.g., Hubbs and Schultz 1929; Hubbs 1948; Radovich 1960; Pearcy and Schoener 1987). Passive transport has been documented for holoplanktonic organisms and species with dispersive larval stages (e.g., Glynn 1961; Pearcy and Schoener 1987; Bertsch et al. 2000), and it is possible for some brooding invertebrates to raft on algal mats (Highsmith 1985). These species are rarely observed and only during the ENSO event. In this study, four species were rarely found, but only the range record of *Polycera alabe* is concordant with a particular ENSO event. This nudibranch was not seen at Santa Catalina Island until the 1997–98 ENSO event, when two adults were collected in summer 1998 near the intake pipes at the Wrigley Institute for Environmental Studies (Fig. 1). In fall 1998, the observation of a single *P. alabe* at Santa Barbara Island and Anacapa Island, both north of Santa Catalina Island, and its absence at those sites from 1982 to 1997 and after 1998 (D. Richards personal communication) further support this as an ephemeral occurrence due to the 1997–98 ENSO event. In addition, three new northern records of other opisthobranchs were reported along the coast of Baja California during the 1997–98 ENSO event (Bertsch et al. 2000), suggesting *P. alabe* was one of several opisthobranch species responding to the ENSO event.

Second, southern larval recruits may establish northern relict populations (Hutchins 1947) that persist after the ENSO event but slowly decline in abundance and eventually disappear. These small, isolated populations should consist primarily of species capable of long-ranging dispersal and should have only one or a few size classes indicative of infrequent recruitment. At our study sites *Maxwellia gemma, M. santarosana, Odostomia eucosmia,* and *Turbonilla kelseyi* were uncommon and consisted almost exclusively of adults, which suggests these species represent ENSO-related relict populations. Because we know of no size-age relationships for these species, we cannot estimate time of settlement to determine if it corresponds to a previous ENSO event.

Third, the recruitment of larvae produced by southern "source" populations may sustain persistent extralimital "sink" populations that have little or no local reproductive success during normal oceanic conditions (Mileikovsky 1971; Lewis et al. 1982). For example, recruitment of barnacle larvae to the intertidal within their geographic range was higher than normal during the onset of the 1997–98 ENSO event along central California (Connolly and Roughgarden 1999). As a corollary of their study, recruitment was also higher beyond the northern range limit of these barnacles. Marginal populations are expected to have more age- and size-classes than relict populations, some missing cohorts, and a bias towards larger and older individuals (Lewis et al. 1982). For example, *Kelletia kelletii* (Kellet's whelk) in Monterey Bay generally fits this pattern, with no recruits (<15 mm), few juveniles (20–40 mm), and many large (70–100 mm) adults (Lonhart unpublished data). The lack of local reproductive success in Monterey Bay suggests this whelk population is dependent upon recruits from southern California during years of anomalous oceanic conditions. In the present study, populations of both *Norrisia norrisi* and *Ophiactis simplex* were almost certainly transported northward to Diablo Cove during past ENSO events. However, the establishment and maintenance of populations in Diablo Cove has been facilitated by thermal effluent from DCPP (see below). It remains unclear whether the thermal discharge allows larvae from southern California to recruit and settle, or supports local reproduction, or does both.

Alternative Mechanisms

Despite the strong impact of ENSO events on species distribution, additional factors that impact the known distribution of organisms must be considered. The significance and effects of these additional factors, which include anthropogenic introductions and climatic warming, are discussed in detail elsewhere (Lonhart and Tupen in prep.). Here we present a summary of the effects of thermal refugia and sampling artifacts. Thermal refugia are localized areas of consistently anomalous sea surface temperature that allow populations to survive in relatively small, isolated areas separated from their native range by stretches of thermally unacceptable waters (Dawson 1945; Hubbs 1948; Lindberg 1991). The Diablo Canyon Power Plant began full operation in 1986, creating a year-round thermal plume in Diablo Cove (4–5°C above ambient) that closely resembles the warm-temperate waters of southern California. We propose that of the 12 species presented here, only *Norrisia norrisi* and *Ophiactis simplex* are truly responding to the thermal plume: both are found only in the thermally elevated parts of Diablo Cove and invaded (*O. simplex*) or increased in abundance (both species) after DCPP operation began (Lonhart and Tupen in prep.).

Existing range data are likely incomplete for all but a few well-studied species because of sampling artifacts. There are three general explanations: (1) the spatial and temporal scale of most studies is extremely limited; (2) the taxonomy and ecology of most species is poorly known; and (3) new range records deposited in museum collections are infrequently published. Not surprisingly, collection trips to poorly studied or remote areas often discover new range records (e.g., Vermeij et al. 1990; Bertsch et al. 2000). In this study, eight new range records were from Diablo Cove, which has limited public access. Although pre- and post-operational studies at Diablo Cove cover a limited spatial scale, they have been ongoing since 1976 (Tenera 1997). Unpublished museum records for four species (*Trivia solandri, Opalia funiculata, Nucella canaliculata,* and *Odostomia eucosmia*) were beyond those reported in the literature and our study sites.

We have shown that only one of 12 new range records is the result of the 1997–98 ENSO event, and that other mechanisms, such as thermal refugia and sampling artifacts, have contributed to the presence of the remaining 11 species beyond their known geographic range. Understanding how various factors alter our knowledge of the spatial and temporal extent of a species' geographic range is an important first step towards designing research programs that accurately monitor the effects of habitat loss and species invasions, assess native biodiversity, and study biological responses to climate change.

Acknowledgements

We thank Jim McLean, Lindsey and Cathy Groves, Gordon Hendler, Don Cadien, and George Davis (LACM); Henry Chaney, Paul Scott, and Patricia Sadeghian (SBMNH); Eugene Coan, Liz Kools, Chris Mah, and Bob Van Syoc (CAS); Carole Hertz and Tom Demere (SDNHM); Al Chadwick and Tim Pearce (DMNH); and Gary Rosenberg (ANSP) for taxonomic and range verifications and voucher material deposition. We acknowledge the assistance of Mike Behrens and Jay Carroll (TENERA) in the field, and Dan Richards (Channel Islands National Park Service) for unpublished data. We also thank Jim McLean, Alan Miller, John Pearse, Don Potts, Pete Raimondi, Kerstin Wasson, and an anonymous reviewer for constructive comments on earlier versions of the manuscript.

Literature Cited

Abbott, R. T. 1974. American seashells, 2nd edition. Van Nostrand Reinhold, 663 pp.

Behrens, D. W. 1991. Pacific Coast nudibranchs: a guide to the opisthobranchs, Alaska to Baja California. Sea Challengers, vi + 107 pp.

Bertsch, H., O. A. Campillo and J. L. Arreola. 2000. New distributional records of opisthobranchs from the Punta Eugenia region of the Baja California peninsula: a report based on 1997–1998 CONABIO-sponsored expeditions. Festivus, 32: 99–104.

Brown, J. H., G. C. Stevens and D. M. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. Ann. Rev. Ecol. Syst., 27: 597–623.

Carlton, J. T. and J. B. Geller. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. Science, 261: 78–82.

Coan, E. V., P. H. Scott and F. R. Bernard. 2000. Bivalve seashells of western North America: marine bivalve mollusks from Arctic Alaska to Baja California. Santa Barbara Mus. Nat. Hist., viii + 764 pp.

Cohen, A. N. and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science, 279: 555–558.

Collin, R. and J. B. Wise. 1997. Morphology and development of *Odostomia columbiana* Dall and Bartsch (Pyramidellidae): implications for the evolution of gastropod development. Biol. Bull., 192: 243–252.

Connolly, S. R. and J. Roughgarden. 1999. Increased recruitment of northeast Pacific barnacles during the 1997 El Niño. Limnol. Oceanog., 44: 466–469.

Cumming, R. L. 1993. Reproduction and variable larval development of an ectoparasitic snail, *Turbonilla* sp. (Pyramidellidae, Opisthobranchia), on cultured giant clams. Bull. Mar. Sci., 52: 760–771.

Dawson, E. Y. 1945. Marine algae associated with upwelling along the northwestern coast of Baja California, Mexico. Bull. So. Cal. Acad. Sci., 44: 57–71.

Dayton, P. K. and M. J. Tegner. 1990. Bottoms beneath troubled waters: benthic impacts of the 1982–

84 El Niño in the temperate zone. Pp. 433–472 *in* Global ecological consequences of the 1982–83 El Nino-Southern Oscillation. (P. W. Glynn, ed.), Elsevier, xx + 563 pp.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, 181 pp.

Fotheringham, N. 1971. Life history patterns of the littoral gastropods *Shaskyus festivus* (Hinds) and *Ocenebra poulsoni* Carpenter (Prosobranchia: Muricidae). Ecology, 52: 742–757.

Glynn, P. W. 1961. The first recorded mass stranding of pelagic red crabs, *Pleuroncodes planipes,* at Monterey Bay, California, since 1859, with notes on their biology. Cal. Fish and Game, 47: 97–101.

Glynn, P. W. 1990. Global ecological consequences of the 1982–83 El Nino-Southern Oscillation. Elsevier, xx + 563 pp.

Highsmith, R. C. 1985. Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. Mar. Ecol. Prog. Ser., 25: 169–179.

Hubbs, C. L. 1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. J. Mar. Res., 7: 459–482.

Hubbs, C. L. and L. P. Schultz. 1929. The northward occurrence of southern forms of marine life along the Pacific coast in 1926. Cal. Fish and Game, 15: 234–241.

Hutchins, L. W. 1947. The bases for temperature zonation in geographical distribution. Ecol. Mono., 17: 325–335.

Lewis, J. R., R. S. Bowman, M. A. Kendall and P. Williamson. 1982. Some geographical components in population-dynamics: possibilities and realities in some littoral species. Neth. J. Sea Res., 16: 18–28.

Lindberg, D. R. 1991. Marine biotic interchange between the northern and southern hemispheres. Paleobiol., 17: 308–324.

McGowan, J. A., D. R. Cayan and L. M. Dorman. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. Science, 281: 210–217.

McLean, J. H. 1978. Marine shells of southern California. Nat. Hist. Mus. Los Angeles Co., 104 pp.

McPhaden, M. J. 1999. El Niño—The child prodigy of 1997–98. Nature, 398: 559, 561–562.

Mileikovsky, S. A. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. Mar. Biol., 10: 193–213.

Morris, R. H., D. P. Abbott and E. C. Haderlie. 1980. Intertidal invertebrates of California. Stanford Univ. Press, ix + 690 pp.

Norton, J., D. McLain, R. Brainard and D. Husby. 1985. The 1982–83 El Niño event off Baja and Alta California and its ocean climate context. Pp. 44–72 *in* El Niño north: Niño effects in the eastern subarctic Pacific Ocean. (W. S. Wooster and D. L. Fluharty, eds.), Wash. Sea Grant Prog. Univ. Wash., v + 312 pp.

Pearcy, W. G. and A. Schoener. 1987. Changes in the marine biota coincident with the 1982–1983 El Niño in the northeastern subarctic Pacific Ocean. J. Geophys. Res.-Oceans, 92: 14417–14428.

Radovich, J. 1960. Redistribution of fishes in the eastern north Pacific Ocean in 1957 and 1958. Cal. Coop. Oceanic Fish. Invest., 7: 163–171.

Richmond, R. H. 1990. The effects of the El Niño/Southern Oscillation on the dispersal of corals and other marine organisms. Pp. 127–140 *in* Global ecological consequences of the 1982–83 El Nino-Southern Oscillation. (P. W. Glynn, ed.), Elsevier, xx + 563 pp.

Tenera. 1997. Changes in the marine environment resulting from the Diablo Canyon Power Plant discharge. Diablo Canyon Power Plant: Thermal effects monitoring program analysis report, Chapter 1, Technical Report E7-204.7. Tenera Environmental Services.

Thurman, H. V. 1985. Introductory oceanography. Merrill Pub. Co., vii + 503 pp.

Vermeij, G. J. 1991. When biotas meet: understanding biotic interchange. Science, 253: 1099–1104.

Vermeij, G. J., A. R. Palmer and D. R. Lindberg. 1990. Range limits and dispersal of mollusks in the Aleutian Islands, Alaska. Veliger, 33: 346–354.

Wooster, W. S. and D. L. Fluharty. 1985. El Niño north: Niño effects in the eastern subarctic Pacific Ocean. Wash. Sea Grant Prog. Univ. Wash., v + 312 pp.

Accepted for publication 21 December 2000.

Bull. Southern California Acad. Sci.
100(3), 2001, pp. 249–251

INDEX TO VOLUME 100

Allen, M. James. First Occurrence of Blackspot Wrasse, *Decodon melasma* Gomon 1974 (Pisces: Labridae) in California. 131
Allen, M. James. First Occurrence of Speckletail Founder, *Engyophrys sanctilaurentii* Jordan & Bollman 1890 (Pisces: Bothidae), in California. 137
Allen, M. James, see Ami K. Groce
Allen, M. James, see Daniel J. Pondella II
Applegate, Shelton P., see Harry L. Fierstine
Armitage, Mark, Cercarial Emergence from Rediae in California Snail Tissues. 51
Arrubarrena, Luis Espinosa, see Harry L. Fierstine

Bell, Christopher J., see Jim I. Mead
Boyle, Kelly, see Robert N. Lea
Bursey, Charles R., see Stephen R. Goldberg

Cadien, Donald B., see David E. Montagne
Chase, Shawn D., Contributions to the Life History of Adult Pacific Lamrey (*Lampetra tridentata*) in the Santa Clara River of Southern California. 74
Craig, Matthew T., see Daniel J. Pondella II.
Curtis, Michael D., First Record of the Pacific Cornetfish, *Fistularia corneta* Gilbert and Starks 1904, a New Species to the Southern California Fauna During the 1997–1998 El Niño. 156

Davis, Jana L. D., Spot Pattern of *Girella nigricans,* the California Opaleye: Variation among Cohorts and Climate Periods. 24

Engle, John M., New and Unusual Marine Invertebrates Discovered at the California Channel Islands during the 1997–1998 El Niño. 186
Engle, John M., see Daniel V. Richards
Erikson, Erik D., see Robert N. Lea

Fierstine, Harry L., A Fossil Blue Marlin (*Makaira nigricans* Lacépède) from the Middle Facies of the Trinidad Formation (Upper Miocene to Upper Pliocene), San José del Cabo Basin, Baja California Sur, México. 59

Given, Robert, see Robert N. Lea
Goldberg, Stephen R., Persistence of the Nematode, *Oswaldocruzia pipiens* (Molineidae), in the Pacific Treefrog, *Hyla regilla* (Hylidae), from California. 44
Goldberg, Stephen R., Helminths of Six Species of Colubrid Snakes from Southern California. 109
Goldberg, Stephen R., Helminths of the California Treefrog, *Hyla cadaverina* (Hylidae), from Southern California. 117
González-Barba, Gerardo, see Harry L. Fierstine
Grismer, L. Lee, An Evolutionary Classification and Checklist of Amphibians and Reptiles on the Pacific Islands of Baja California, México. 12

Groce, Ami K. Addition of Blacklip Dragonet, *Synchiropus atrilabiatus* (Garman, 1899) (Pisces: Callionymidae) to the California Ichthyofauna. 149
Groce, Ami K. Addition of the Calico Lizardfish, *Synodus lacertinus* Gilbert, 1890 (Pisces: Synodontidae) to the Ichthyofauna of the Southern California Bight. 153
Groce, Ami K., see M. James Allen

Herbinson, Kevin T., see Michael D. Curtis
Horn, Michael H., see Erick A. Sturm

Lagos, Steven L., see Ami K. Groce
Lea, Robert N., Occurrence of the Loosetooth Parrotfish, *Nicholsina denticulata* (Scaridae), from Santa Catalina Island, California. 167
Lei, Simon A., Diversity of Parasitic *Cuscuta* and their Host Plant Species in a *Larrea-Atriplex* Ecotone. 36
Lei, Simon A., Combined Effects of Drought and *Phoradendrom juniperinum* Infestation Severity on Fruit Characteristics of *P. juniperinum* and its *Juniperus osteosperma* Hosts. 86
Lei, Simon A., Spatial Distribution of Blackbrush (*Coleogyne ramosissima* Torr.) Populations in the Mojave Desert. 96
Lei, Simon A., Postfire Seed Bank and Soil Conditions in a Blackbrush (*Coleogyne ramosissima* Torr.) Shrubland. 100
Lonhart, Steve I., New Range Records of 12 Marine Invertebrates: The Role of El Niño and Other Mechanisms in Southern and Central California. 238

Mead, Jim I., Pliocene Amphibians and Reptiles from Clark County, Neveda. 1
Montagne, David E., Northern Range Extensions into the Southern California Bight of Ten Decapod Crustacea Related to the 1991/92 and 1997/98 El Niño Events. 199

Nestler, Eric C., see Ami K. Groce

Pondella, Daniel J. II. Proceedings of Special Symposium: New and Rare Fish and Invertebrate Species to California during the 1997–1998 El Niño. 129
Pondella, Daniel J. II. First record of the sabertooth blenny, *Plagiotremus azaleus,* in California, with notes on its distribution along the Pacific coast of Baja California. 144

Reiswig, Henry M., A New North Pacific *Heterochone* Transferred from *Aphrocallistes* (Porifera: Hexactinellida). 123
Richards, Daniel V., New and Unusual Reef Fish Discovered at the California Channel Islands During the 1997–1998 El Niño. 175
Richards, Daniel V., see John M. Engle
Rosenblatt, Richard H., see Ami K. Groce

Schwennicke, Tobias, see Shelton P. Applegate
Shane, Michael A., Records of Mexican Barracuda, *Sphyraena ensis,* and Scal-

loped Hammerhead, *Sphyrna lewini,* from Southern California Associated with Elevated Water Temperatures. 160
Sturm, Erick A. Increase in Occurrence and Abundance of Zebraperch (*Hermosilla azurea*) in the Southern California Bight in Recent Decades. 170

Tupen, Jeff W., see Steve I. Lonhart

West, Janelle M., see Gregory D. Williams
Williams, Gregory D., Shifts in Fish and Invertebrate Assemblages of Two Southern California Estuaries during the 1997–98 El Niño. 212

Zedler, Joy B., see Gregory D. Williams

New and Unusual Reef Fish Discovered at the California Channel Islands During the 1997–1998 El Niño. Daniel V. Richards and John M. Engle 175

New and Unusual Marine Invertebrates Discovered at the California Channel Islands during the 1997–1998 El Niño. John M. Engle and Daniel V. Richards 186

Northern Range Extensions into the Southern California Bight of Ten Decapod Crustacea Related to the 1991/92 and 1997/98 El Niño Events. David E. Montagne and Donald B. Cadien 199

Shifts in Fish and Invertebrate Assemblages of Two Southern California Estuaries during the 1997–98 El Niño. Gregory D. Williams, Janelle M. West, and Joy B. Zedler 212

New Range Records of 12 Marine Invertebrates: The Role of El Niño and Other Mechanisms in Southern and Central California. Steve I. Lonhart and Jeff W. Tupen 238

Index to Volume 100 249

CONTENTS

Proceedings of Special Symposium: New and Rare Fish and Invertebrate Species to California during the 1997–1998 El Niño. Daniel J. Pondella, II and M. James Allen, Editors 129

First Occurrence of Blackspot Wrasse, *Decodon melasma* Gomon 1974 (Pisces: Labridae) in California. M. James Allen and Ami K. Groce 131

First Occurrence of Speckletail Flounder, *Engyophrys sanctilaurentii* Jordan & Bollman 1890 (Pisces: Bothidae), in California. M. James Allen and Ami K. Groce 137

First record of the sabertooth blenny, *Plagiotremus azaleus*, in California with notes on its distribution along the Pacific coast of Baja California. Daniel J. Pondella, II and Matthew T. Craig 144

Addition of Blacklip Dragonet, *Synchiropus atrilabiatus* (Garman, 1899) (Pisces: Callionymidae) to the California Ichthyofauna. Ami K. Groce, Richard H. Rosenblatt, and M. James Allen 149

Addition of the Calico Lizardfish, *Synodus lacertinus* Gilbert, 1890 (Pisces: Synodontidae) to the Ichthyofauna of the Southern California Bight. Ami K. Groce, Steven L. Lagos, and Eric C. Nestler 153

First Record of the Pacific Cornetfish, *Fistularia corneta* Gilbert and Starks 1904, a New Species to the Southern California Fauna During the 1997–1998 El Niño. Michael D. Curtis and Kevin T. Herbinson 156

Records of Mexican Barracuda, *Sphyraena ensis*, and Scalloped Hammerhead, *Sphyrna lewini*, from Southern California Associated with Elevated Water Temperatures. Michael A. Shane 160

Occurrence of the Loosetooth Parrotfish, *Nicholsina denticulata* (Scaridae), from Santa Catalina Island, California. Robert N. Lea, Erik D. Erikson, Kelly Boyle, and Robert Given 167

Increase in Occurrence and Abundance of Zebraperch (*Hermosilla azurea*) in the Southern California Bight in Recent Decades. Erick A. Sturm and Michael H. Horn 170

COVER: *Loosetooth parrotfish from Santa Catalina Island. Photo by E. Erikson*